Grouping Behaviour in the Armadillo Girdled Lizard,

Cordylus cataphractus

by

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Declaration: I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

- ABSTRACT -

Cordylus cataphractus and *C. macropholis* naturally occur in groups on a year round basis. I examined whether limited shelter availability might be responsible for this phenomenon. Individuals were provided with an excess of shelter sites and the observed pattern of shelter occupation was contrasted to that obtained for the solitary living species *C. polyzonus*. *Cordylus cataphractus* consistently occupied fewer shelters than its two congeners. Results suggest that grouping behaviour in this species is not the result of a limitation in refuge sites. In contrast, the pattern of shelter occupation by *C. macropholis* did not differ significantly from that of *C. polyzonus*, thus the aggregative behaviour observed in the former species may partially be attributed to limited shelter availability in its natural habitat.

Conspecific recognition by means of pheromonal detection has been reported in many lizard families, but only for one member of Cordylidae, namely *Cordylus cordylus*. *Cordylus cataphractus* individuals were exposed to ceramic tiles that had been labeled by conspecific male and female substrate deposits. Labeling was achieved by using ceramic tiles as the bottom half of a shelter in a lizard's home cage for ten consecutive days. Washed tiles were used as controls. Labeled tiles did not elicit significantly more tongue-flicks than control tiles from test specimens in a series of trials. The apparent lack of conspecific recognition via pheromonal detection might be attributable to the group-living nature of this species, which primarily use visual cues for identification purposes. Tongue-flicking is generally utilized in *C. cataphractus* in the detection of novel stimuli.

Spatial dynamics of the group-living cordylid, *C. cataphractus*, were investigated by studying patterns of intergroup movement. To date, literature has assumed that *C. cataphractus* groups represent family units, implying low or delayed dispersal rates and high group fidelity. A mark-recapture experiment on six groups included three recaptures outside

of and three recaptures within the mating season. High percentages of male, female and juvenile lizards left their groups, but might be an artifact of microhabitat disturbance. High proportions of males, females and juveniles entering the groups, both outside of and within the mating season, clearly implied a high rate of intergroup movement.

Activity and foraging patterns were studied in group-living *C. cataphractus* lizards by conducting direct field observations between September 1998 and October 1999. The influence of general weather patterns as well as the effect of group size on these patterns were investigated by observing a small-sized, medium-sized and large group. Each group was observed for a minimum of three sunny days per season, with scans conducted every 30 minutes between the hours of 08:00 and 20:00. There was a high rate of activity during the mating season in spring (September). Activity declined sharply and foraging ceased at the onset of warm, dry conditions (February). Virtually no activity occurred just prior to the first winter rains (July), after which the lizards emerged to forage and replenish energy stores before onset of the next mating season. Selective inactivity might be employed to reduce energy expenditure in this group-living lizard, where intraspecific competition is stringent. Groups of different sizes display different thresholds at which it becomes energetically viable for group members to emerge, as well as different patterns of spatial use around their respective home crevices. Members of larger groups perched further from their crevices, ran further to catch prey and had less potential prey capture events per individual. Lizards in the larger groups also displayed sporadic lengthy foraging excursions. Such movements might explain the evolution of tail-biting behaviour and heavy armour, which are defensive strategies associated with open areas.

- UITTREKSEL -

Cordylus cataphractus en *C. macropholis* word dwarsdeur die jaar in groepe in hul natuurlike habitat aangetref. Daar is nagevors of 'n beperking in aantal beskikbare skuilplekke vir hierdie verskynsel verantwoordelik is. Individue is van 'n oormaat skuilings voorsien en die waargenome patroon van skuilplekbesetting is gekontrasteer met dié verkry vir 'n enkelwonende species, naamlik *C. polyzonus*. *Cordylus cataphractus* het voortdurend minder skuilplekke beset as sy kongeneriese species. Groepsgedrag in *C. cataphractus* is dus nie die resultaat van 'n tekort aan beskikbare skuilplekke nie. In teenstelling hiermee het die patroon van skuilplekbesetting vertoon deur *C. macropholis* nie noemenswaardig verskil van dié van *C. polyzonus* nie. Dus mag die groepsgedrag wat gewoonlik in *C. macropholis* waargeneem word 'n uitvloeisel wees van 'n beperking op die beskikbaarheid van skuilplekke in sy natuurlike habitat.

Herkenning van speciesgenote deur waarneming van feromone is vir verskeie akkedisfamilies gerapporteer, maar slegs vir een lid van Cordylidae, naamlik *C. cordylus*. *Cordylus cataphractus* individue is blootgestel aan keramiekteëls wat gemerk is met substraat-neerleggings van manlike en vroulike speciesgenote. Sodanige merking is uitgevoer deur die keramiekteëls vir tien dae lank te gebruik as die onderste helfte van akkedisse se skuilplekke in hul tuishokke. Gewaste teëls is as kontroles gebruik. Gemerkte teëls het nie statisties beduidend meer tongskiete van die akkedisse uitgelok as kontrole teëls in 'n reeks toetse nie. Die klaarblyklike afwesigheid van speciesgenootherkenning deur middel van feromoon waarneming kan moontlik toegeskryf word aan die groeplewende gedrag van *C. cataphractus*, wat primêr visuele informasie vir identifikasie gebruik. *Cordylus cataphractus* gebruik tongskiete oor die algemeen vir die waarneming van nuwe omgewingsstimuli.

Die ruimtelike dinamika van 'n groeplewende gordelakkedis, *C. cataphractus*, is ondersoek deur die patroon van intergroepbeweging na te vors en groepsgetrouheid te meet.

Tot op datum is daar in die literatuur aanvaar dat *C. cataphractus* groepe familie-eenhede verteenwoordig, wat lae of vertraagde verpreidingstempo's asook 'n hoë mate van groepsgetrouheid impliseer. 'n Merk-hervang eksperiment is op ses groepe uitgevoer, insluitend drie hervang episodes buite en drie binne die paarseisoen. 'n Hoë persentasie manlike, vroulike en onvolwasse akkedisse het hul groepe verlaat, maar dit mag bloot 'n uitvloeisel van versteuring van die mikrohabitat wees. 'n Hoë proporsie mannetjies, wyfies en onvolwassenes het egter by die groepe aangesluit, beide buite en binne die paarseisoen, wat onteenseglik op 'n hoë mate van intergroep beweging dui. Daar kom derhalwe veel vryer bewegingspatrone in hierdie species voor as voorheen vermoed en dit is hoogs onwaarskynlik dat groepe familie-eenhede verteenwoordig.

Aktiwiteits- en voedingspatrone van die groeplewende akkedis, *C. cataphractus*, is bestudeer in 'n reeks veldobservasies tussen September 1998 en Oktober 1999. Afgesien van die invloed van algemene weerspatrone, is die effek van groepgrootte op hierdie patrone ondersoek deur 'n klein, medium en groot groep te observeer. Elke groep is waargeneem oor 'n minimum periode van drie dae per seisoen met opnames elke 30 minute, tussen 08:00 ten 20:00. 'n Hoë aktiwiteitsvlak is gedurende lente tydens die paarseisoen gehandhaaf (September). Met die aanvang van warm en droë kondisies (Februarie) het aktiwiteitsvlakke skerp begin daal en voedingsgedrag is gestaak. Feitlik geen aktiwiteit was waarneembaar kort voor die eerste winterreëns (Julie) nie, waarná akkedisse intensief begin voed het om energiestore op te bou voor die aanvang van paartyd. Selektiewe onaktiwiteit verminder moontlik energieverbruik in hierdie groeplewende akkedis, waar intraspesifieke kompetisie streng is. Verskillende groepgroottes beskik oor verskillende perke waar dit vir die individu energeties voordelig sou wees om uit die skeur te kom, asook 'n variasie in ruimtelike gebruik om die skeur.

Individue van die twee groter groepe het nader aan hul rotsskeur gesit, het verder van die skeur af prooi vang en het beduidend minder potensiële voedingskanse gehad. Akkedisse in die groter groepe het voorts sporadiese lang voedingsekskursies getoon. Hierdie bewegings mag die evolusie van stertbytgedrag en 'n swaar pantser, verdedigingstrategieë wat met oop areas geassosieer word, verduidelik.

Dedication: In memory of my father, Giel Geldenhuys Visagie.

- ACKNOWLEDGEMENTS -

Cataphractus -a –um (L., adj.) mail-clad; *cataphractus -i* (L., n.) cavalryman clad in chain mail from the top of his head to his toes, with his horse also covered in chain mail; peculiar to Armenian and Parthian armies of 50 B.C. (McCullough, 1998).

Cordylus cataphractus truly deserves its scientific name, in more than the intended descriptive sense. A war of sorts was indeed waged and I would like to extend my gratitude to the following people and organizations whose various contributions made this project possible. The Foundation for Research and Development provided the major body of funding for my research (NRF grant awarded to P. le F. N. Mouton), supplemented by a Murray Bursary received from the University of Stellenbosch. My two supervisors, le Fras Mouton and Alex Flemming, instilled me with a great passion for herpetology and I thank them for their continued guidance and endless patience. A special word of gratitude is also due for Dirk Bauwens of the Institute of Nature Conservation in Belgium; his statistical advice, positive criticism and words of encouragement never ceased to be a source of inspiration.

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- PREFACE -

THIS study is part of ongoing research that is currently being conducted on Cordylidae at the Zoology department of the University of Stellenbosch. More specifically, I will focus on a member of the genus Cordylus, namely, *Cordylus cataphractus.* To date, empirical research conducted on this genus have focused on questions in diverse fields of study, such as taxonomy and phylogeny (e.g. FitzSimons 1943; Loveridge 1944; Lang 1991; Mouton & Van Wyk 1997; Frost *et al.* 2001), ecomorphology (e.g. Mouton 1987; Mouton & Oelofsen 1988), sexual dimorphism (FitzSimons 1943; Lang 1991; Cordes *et al.* 1995), reproduction (e.g. Van Wyk 1989; Van Wyk 1990; Flemming & Van Wyk 1992; Van Wyk & Mouton 1998), spatial ecology (e.g. Van Wyk 1992; Mouton *et al.* 1999; Ruddock *et al.* in press), foraging ecology (e.g. Cooper *et al.* 1997; Mouton *et al.* 2000c) behaviour (Wirminghaus 1990; Van Wyk 1992; Cooper *et al.* 1996), energetics (e.g. Laburn *et al.* 1981; Bauwens *et al.* 1999; Mouton *et al.* 2000b) and conservation (Mouton *et al.* 1987; Jacobsen *et al.* 1990). Yet much remains unknown, not only of this genus, but in fact of the entire family of lizards, as apparent in the absence of adequate information on cordylids in herpetological literature.

The work contained in this thesis addresses various aspects regarding the ecology and behaviour of the armadillo girdled lizard, *Cordylus cataphractus*. What makes this South African endemic particularly noteworthy is the fact that it displays the clearest manifestation of grouping behaviour observed in any lizard species to date. My research questions therefore focus either on grouping behaviour directly or on the possible effects of grouping behaviour on the behavioural ecology of armadillo lizards (as opposed to the scenario encountered among solitary-living congeners).

Owing to the grouping behaviour exhibited by *C. cataphractus*, results presented here not only add to our understanding of cordylids per se, but also provide new information on sociality among lizards in general. The latter subject is receiving increasing attention, with

research currently being conducted on Australian scincid species of the genus *Egernia*, where grouping behaviour is similarly encountered. Cordylids present an equally ideal opportunity for studies on lizard sociality, displaying a broad spectrum of social structures and behaviours. *Cordylus cataphractus*, specifically, is thought to possess a complex social system. Information on daily and annual activity levels of the species, as presented here in Chapter 4, provides a basis from which future investigations into sociality can be structured more efficiently.

Comprehensive knowledge of the life history of *C. cataphractus* is of value outside a purely academic sphere. Armadillo lizards, due to their attractive nature and the ease with which they adapt to captive conditions, have proven to be extremely popular pets among amateur herpetologists. This resulted in the export of large numbers of lizards to, for instance, Germany in the early 1930's (Loveridge 1944) and the Netherlands between 1960 and 1970 (unpublished data). *Cordylus cataphractus* occurs within a fairly limited range and has since been listed as "vulnerable" in the South African Red Data Book for Reptiles and Amphibians (Branch 1988b), with a ban on trade in the species in effect since 1980. Combined with the relative ease with which these sluggish lizards are found and captured, illegal collection of specimens has continued. The measure of exploitation of *C. cataphractus* and true impact of illegal trade on its numbers remain uncertain (Mouton *et al.* 1987). Proper knowledge of the life history of armadillo lizards however ensures structuring of a manageable conservation strategy, should it become necessary.

My thesis is structured as follows. A general introduction provides background information on the family Cordylidae as well as a brief description of *C. cataphractus*, in order to avoid unnecessary repetitions in the introductions of the subsequent four chapters. Chapters 1 and 2 present results on two controlled behavioural experiments that were conducted at the University of Stellenbosch. Of these, Chapter 1 has been submitted for

publication (particulars in the footnote on page 1). Chapters 3 and 4 are concerned with fieldwork experiments, with Chapter 4 encompassing the first extensive observations of armadillo lizards in their natural habitat. The general summary reiterates the major findings of this project and provides a global perspective thereof, also posing a number of questions that still remain unanswered. Lastly, Appendix A contains data collected from a group of 40 lizards that were collected and released during the course of my studies, since this represents the largest group of this species that has been collected to date.

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- GENERAL INTRODUCTION -

CORDYLIDAE is a scincomorph family of lizards endemic to sub-Saharan Africa, with a distinct clustering of species in the south (Mouton & Van Wyk 1997). The 50 odd species in this family have traditionally been partitioned into four nominal genera (Loveridge 1944; Branch 1998): *Platysaurus* (flat lizards), *Cordylus* (girdled lizards), *Pseudocordylus* (crag lizards), and *Chamaesaura* (grass lizards). This classification is currently under revision. Frost *et al.* (2001) recently incorporated results of molecular analyses into an existing character database containing mainly morphological traits (Lang 1991; Harvey & Gutberlet 1995). The authors conclude that *Platysaurus* is the sister taxon of all remaining cordylids and suggest that both *Chamaesaura* and *Pseudocordylus* be transferred to the genus *Cordylus* to render a monophyletic taxonomy (see Frost *et al.* 2001). To avoid any confusion, I will however adhere to the traditional classification system in my thesis.

Cordylids are typical sit-and-wait foragers, lacking the ability to discriminate prey chemicals by means of tongue-flicking behaviour (Branch 1988a; Cooper *et al.* 1997). *Platysaurus*, regarded as the basal cordylid genus (Mouton & Van Wyk 1997; Frost *et al.* 2001), differs from all other cordylids in being oviparous and displaying mainly subtropical or lowland distribution (Mouton & Van Wyk 1997). They are strictly rupicolous lizards with highly dorsoventrally flattened bodies, enabling them to inhabit narrow crevices created by flaking rocks (Branch 1998). Several *Platysaurus* spp. are gregarious and aggregate in dense colonies, most clearly illustrated by the dense feeding aggregations formed by *P. broadleyi* (Broadley 1978; Branch & Whiting 1997; Branch 1998). In the *Cordylus-Pseudocordylus-Chamaesaura* clade, viviparity evolved as an adaptation to cold climates, apparent in the highland or temperate distribution of extant species (Mouton & Van Wyk 1997). Members of the genus *Cordylus* are stocky, often spinose lizards with large, osteodermate scales arranged in regular girdles around their bodies (Branch 1998). Most girdled lizards are rupiculous,

with the exception of a few terrestrial species, e.g. *C. macropholis* (Mouton & Van Wyk 1997) and *C. giganteus* (Van Wyk 1992). Solitary living, territorial species occur in either dense or diffuse colonies (Branch 1998), while at least three species are known to display year-round grouping behaviour: *C. peersi* (Branch 1998; Mouton, pers. comm.), *C. macropholis* (Branch 1988a; Mouton *et al.* 2000a), and *C. cataphractus* (Peers 1930; Mouton *et al.* 1999).

Endemic to the west coast of South Africa, *C. cataphractus* (Figure i) occurs from the Orange River in the north to Piketberg in the south, and inland as far as Matjiesfontein in the western Karoo (Mouton *et al.* 1987; Mouton 1988). As described by Peers (1930) and FitzSimons (1943), this is a heavily armoured and thickset lizard, comparatively sluggish in its movements. Its coloration is cryptic, ranging from yellowish-brown to dark brown, with each individual possessing a unique pattern of dark blotches on its throat scales (Peers 1930; Branch 1998; own observations). The lizard is probably best known for the distinctive anti-predatory behaviour to which it owes its common name, the armadillo girdled lizard – when threatened, the lizard rolls into a ball and firmly grasps its tail in its mouth (described in detail by Peers 1930, and Mouton *et al.* 1999).

As mentioned before, *C. cataphractus* is one of three girdled lizards known to display permanent grouping behaviour in its natural habitat (Mouton *et al.* 1999). The exact nature and extent of this grouping phenomenon has been a question of some debate. Peers (1930) was the first to assume that each aggregation consists of a family group sharing a home crevice, containing no more than one adult pair with three or four seasons' progeny. His anecdotal evidence in support of this assumption is that the lizards appear lethargic and that he never observed them far from their crevices. It is now known that large groups may contain more than one adult male, and quite often more than one adult female (Mouton *et al.* 1999; Appendix 1). Yet the assumption that aggregations represent *C. cataphractus* family

groups persists to the present (Branch 1998), although no empirical behavioural or molecular research has ever confirmed this hypothesis.

With regard to group size, Peers (1930) reported a maximum of eight members per group. Recent field surveys have exposed this figure to be a gross underestimate, as groups of up to 30 lizards are often encountered (Mouton *et al.* 2000c). During the course of my own fieldwork, a group of 40 individuals was collected from underneath a relatively small sandstone rock (details provided in Appendix 1). Average group size for *C. cataphractus* varies significantly between localities. Lowland populations of the coastal plains contain larger groups, while populations inland and in more mountainous terrain are characterized by smaller group sizes (own observations). Group composition is at least partially determined by group size, as reported by Mouton *et al.* (1999). Individuals occurring singly are most likely to be males. Groups of two to four individuals contain adult male-female pairs, with or without juveniles. Where group size exceeds four individuals, multiple adult females are often encountered, though it is not uncommon to discover more than one adult male. For instance, one group of 18 individuals included no less than seven adult males, as opposed to only three adult females (Mouton *et al.* 1999).

Being extreme sit-and-wait foragers (Cooper *et al.* 1997; Mouton *et al.* 2000c), groups of *C. cataphractus* lizards are often seen basking on top of sandstone outcrops. The lizards are wary and the entire group will retreat into their crevice at the first sign of danger, possibly making use of the increased vigilance effect (Peers 1930; Mouton *et al.* 1999). No attempts have been made to observe the general behaviour of *C. cataphractus* in its natural habitat, and consequently no data exist on its diurnal and seasonal activity patterns.

It is important to note that both my fieldwork and experimental research were conducted on members of lowland *C. cataphractus* populations, as encountered on the coastal plains. All results, as provided in this thesis, are considered in this light and cannot

necessarily be interpreted as a description of the species as a whole without a certain measure of caution. As mentioned before, group size (and therefore composition) is known to differ between localities - morphological differences are similarly encountered. Lizards of lowland populations attain a larger average snout-vent length, possess fewer generation glands, and have darker coloration than lizards of the higher altitudes (Mouton pers. comm.; own observations). Therefore this work presents a basis from which future comparisons with inland populations can be made, and the words of Peers (1930) still remain true:

> "Here we will have to leave the subject, but these charming creatures will long be waiting up in the West for someone else to make further observations."

FIGURE i - *Cordylus cataphractus*, the armadillo girdled lizard.

- CHAPTER 1 -

EXPERIMENTAL ANALYSIS OF GROUPING BEHAVIOUR IN *CORDYLUS CATAPHRACTUS* AND TWO CONGENERIC SPECIES, C. *MACROPHOLIS* AND *C. POLYZONUS*[1]

ALTHOUGH lizards and snakes generally live solitary lives, temporary aggregations have been described in several species. In temperate zone species, these aggregations may occur during periods of reduced activity, as is found in the formation of winter aggregations in certain *Eumeces*, *Urosaurus* and *Sceloporus* species (Neill 1948; Worthington & Sabath 1966; Weintraub 1968; Ruby 1977). Alternatively, such aggregations serve as a focal point for specific activities and have been termed accordingly. Sheltering (Hoofien 1962; Myres & Eells 1968) and basking (Hoofien 1962; Myres & Eells 1968) aggregations serve a strict thermoregulatory purpose, while mating (Pope 1937; Hoofien 1962) gestating (Graves & Duvall 1993; Seburn 1993) and nesting (Rand 1967; Bock & Rand 1989) aggregations are associated with reproductive behaviour. Feeding aggregations have also been described (Vitt 1974; Arnold & Wassersug 1978). Some authors have even linked the formation of temporary aggregations to possible anti-predatory (Vitt 1974) and water conserving behaviour (Pope 1937; Myres & Eells 1968).

By contrast, few species of lizards exhibit long term or permanent aggregative behaviour. Long term pair-fidelity has been reported in the viviparous skink, *Tiliqua rugosa* (Bull 1994). The Australian scincid genus *Egernia* contains several gregarious species, with aggregations of individuals sharing rock crevices or burrows (Bull *et al.* 2000). Studies on the gidgee skink (*Egernia stokesii*) have shown that, at least in this species, up to 17

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individuals form stable social aggregations and share the same rock crevice for several years (Main & Bull 1996; Bull *et al.* 2000).

Within the African genus *Cordylus*, individuals of both *C. cataphractus* and *C. macropholis* are known to display permanent aggregative behaviour (Branch 1988; Mouton *et al.* 1999; Mouton *et al.* 2000a). In both species, lizards occur in groups on a year round basis, and the grouping tendency is not restricted to any particular season or time of day. The armadillo girdled lizard (*Cordylus cataphractus*) presents the clearest manifestation of grouping behaviour observed within any lizard species to date. *Cordylus cataphractus* is endemic to the arid and semi-arid areas along the west coast of South Africa (Mouton 1988; Branch 1998). On the coastal plains, it inhabits small sandstone outcrops (Peers 1930; Mouton *et al.* 2000c). Groups of up to 40 individuals are encountered occupying a single rock crevice, often containing more than one adult male (Peers 1930; FitzSimons 1943; own observations). *Cordylus macropholis* is a terrestrial form also occurring along the South African west coast. The succulent *Euphorbia caput-medusae* seems to be the preferred microhabitat of this species (Branch 1998; Mouton *et al.* 2000a). Groups of two to five (and occasionally up to eleven) of these lizards can be found sheltering between the stems of the same plant (Mouton *et al.* 2000a; Niewoudt pers. comm.). Only on rare occasions are more than one adult male found within the same plant (Mouton *et al.* 2000a)

Graves & Duvall (1995) reviewed grouping behaviour in squamates and concluded that such aggregations occur as the result of either limited resource availability or mutual attraction of conspecifics, although these two causes are not necessarily mutually exclusive. I aimed to test the hypothesis that aggregation behaviour in *C. cataphractus* and *C. macropholis* is induced by limited shelter availability. Over a large part of the range of *C. cataphractus*, but specifically along the western coastal lowlands, rock outcrops appear to be

a limited resource. Likewise, the distribution of *Euphorbia* plants, considered to be the preferred refuge of *C. macropholis*, is extremely patchy over most of this lizard's range.

I asked whether *C. cataphractus* and *C. macropholis* individuals display a tendency to aggregate when presented with an excess of shelters. Patterns of shelter occupation by these two species were contrasted to that obtained for *C. polyzonus*, a rupiculous form like *C. cataphractus*, but with individuals predominantly found living solitary (Branch 1998). The three species occur sympatrically along the South African west coast. The hypothesis that attributes aggregative behaviour in *C. cataphractus* and *C. macropholis* to limited availability of refuges, predicts that no grouping behaviour will be exhibited when shelter sites are provided in excess. This hypothesis will be supported should individuals of these two species shelter alone and display a pattern of shelter occupation similar to that in *C. polyzonus*. Should *C. cataphractus* or *C. macropholis* exhibit a stronger tendency to aggregate than *C. polyzonus*, my hypothesis will be rejected for that particular species.

MATERIALS AND METHODS

Collection of specimens

Lizards were collected during November 1998 near Lambert's Bay (31° 55' S; 18° 24' E), located along the west coast of South Africa and approximately 300 km north of the University of Stellenbosch. Seven adult males and eight adult females of each species were collected. Size at sexual maturity was taken as 95 mm for *C. cataphractus* (Mouton *et al.* 1999), 58 mm for *C. macropholis* (Mouton *et al.* 2000a) and 89 mm for *C. polyzonus* (Flemming & Van Wyk 1992). Males were distinguished by the presence of large hemipenal bulges, broad heads, and the presence of a relative large number of generation glands (Van Wyk & Mouton 1992). All lizards were released at their site of capture at completion of the experiment.

Housing of Specimens

Specimens were transported to the University of Stellenbosch where they were housed solitarily in glass terraria in a laboratory prior to experimentation. Four weeks were allowed for acclimation to captive conditions. A laboratory window allowed exposure to the natural photoperiod. Room temperature was maintained at 29 °C during daytime, and was allowed to follow ambient temperature at night. Each terrarium was provided with newspaper substrate and with shelter sites constructed from two ceramic tiles separated by two wooden strips. Water and food, primarily tenebrionid larvae, were available *ad libitum*.

Experimental Setup

An open-air experiment was conducted on the roof of a building on the University campus. This provided exposure to the natural photoperiod and weather conditions, and prevented any human interference. Three adjacent square enclosures (330 cm x 330 cm) were demarcated (Figure 1.1). Walls were constructed from asbestos sheets held upright with bricks, delineating the enclosures. Crushed stone was added as substrate. Nine artificial shelters were spaced out in a symmetrical block pattern in each of the three enclosures. A shelter consisted of (top to bottom): a Styrofoam cover (30 x 30 x 8 cm) to reduce radiation heat from the sun; a plywood board (30 x 30 x 2 cm) as shelter cover; three plywood side strips (two 30 x 2 x 2 cm and one 26 x 2 x 2 cm) leaving one side open as a shelter entrance; and an asbestos base (30 x 30 x 0.2 cm). All shelter entrances were north facing. A brick was placed on top of each shelter to stabilize the structure. One food and one water dish was placed in front of and between two shelter openings.

Experimental Procedure

Three consecutive experimental trials (i.e. replicas) were conducted during January 1999.

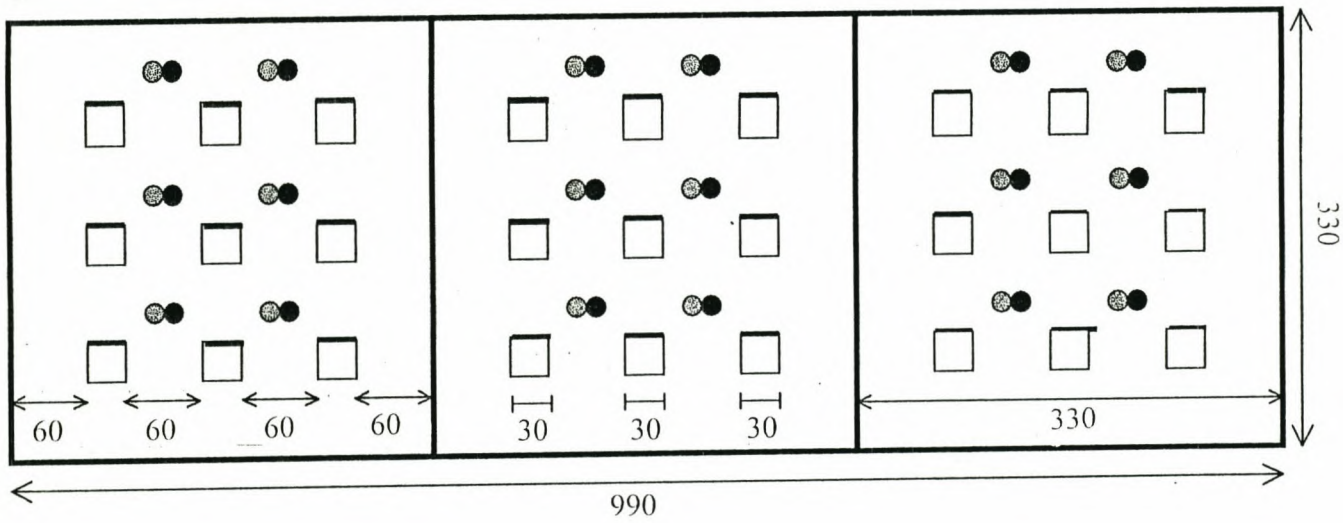

FIGURE 1.1 - Diagram of the experimental setup used to determine whether limited shelter availability influences aggregation in *Cordylus cataphractus*, *C. macropholis* and *C. polyzonus* (details provided in text). Small squares represent individual shelters (30 x 30 cm) with the dark sides representing north-facing shelter entrances. Solid circles represent food dishes and grey circles water dishes. All measurements are in centimeters.

During each trial, which lasted one week, one enclosure was assigned per species. Five lizards were released in each enclosure from a single location therein. The lizards were allowed to acclimate to conditions for a period of 24 hours. During each of the seven following days, the number of lizards residing under each shelter was recorded at 20:00, when all activity for the day had ceased. Fresh water and food were also supplied at this time. On days exceeding 28 °C, the entire experimental area was irrigated at 12:00 and additional drinking water was supplied. Between the three weeklong trials, all shelters were thoroughly washed with water and cleaning agent. The crushed stone substrate was washed with water as well. Different sets of individuals were used in each of the three trials. For each species, two sets consisted of three females and two males, while the remaining set contained three males and two females.

RESULTS

The tendency of the three species to aggregate in shelter sites at night was investigated. As a first approach, each experimental group and each observation night was considered as an independent sample. The test statistic was the number of shelters containing lizards on a given night, ranging between one (i.e., all five lizards under a single shelter) and five (i.e., each lizard sheltering individually). To detect grouping behaviour, the frequency distributions of observed scores for each species were compared to expected Poisson frequencies under the null-hypothesis that lizards shelter individually (i.e., the expected mean value is five occupied shelters). The three species displayed varying degrees of grouping. *Cordylus cataphractus* used two to four shelters per night (Figure 1.2), which is significantly less than expected by the null-hypothesis (Kolmogorov-Smirnov test, $d = 0.56$, $P < 0.01$). On all nights at least two individuals shared a shelter. The maximum number of lizards under a single shelter was four, which was observed on five occasions. *Cordylus macropholis* used a

smaller number of shelters than expected by the null-hypothesis (Kolmogorov-Smirnov test, $d = 0.32$, $P < 0.01$). The discrepancy was largely due to the relatively high frequency of nights in which lizards occupied four shelters (Figure 1.2). This indicates that although the majority of lizards sheltered singly, on rather frequent occasions two lizards shared the same shelter. There were never more than two *C. macropholis* lizards under a single shelter. *Cordylus polyzonus* occupied two to five shelters per night (Fig. 1.2); the observed distribution did not differ from the expected distribution (Kolmogorov-Smirnov test, $d = 0.17$, $P > 0.10$). Lizards predominantly sheltered singly or in pairs, except for one occasion where three *C. polyzonus* individuals were found together.

The former results suggest that *C. cataphractus* and *C. macropholis* exhibited a statistically significant tendency to aggregate under shelters, whereas *C. polyzonus* did not. However, above analyses illegitimately assume that the data for each group of lizards on consecutive nights represent independent samples. This may increase the probability of falsely rejecting the null-hypothesis. To avoid this, a Repeated Measurements ANOVA was used to compare the pattern of shelter occupation by *C. cataphractus* and *C. macropholis* to that of *C. polyzonus*, the species that did not show any tendency to aggregate. This analysis treated the number of shelters occupied on consecutive nights by each experimental group as dependent variables, while "time" (i.e., consecutive nights) served as the within-subjects factor and species as the between-subject factor. There was no significant interaction effect between species and the seven consecutive trial nights ($F = 0.845$; $df = 12, 36$; $P > 0.6$). In other words, any differences in shelter occupation among species remained approximately constant over the experimental period. The number of shelters used by each species did not vary significantly among different nights ($F = 0.270$; $df = 6, 36$; $P > 0.2$). A significant difference was however detected in the number of shelters occupied among the three species

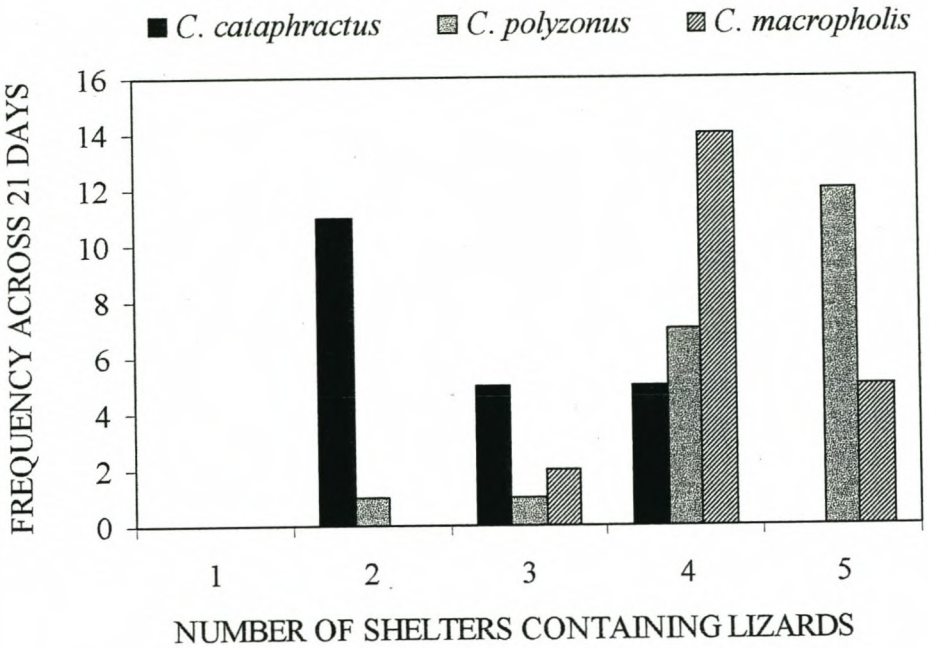

FIGURE 1.2 - Histogram depicting frequencies of shelter occupation by five *Cordylus cataphractus* individuals (diagonal bars), five *C. polyzonus* individuals (solid bars), and five *C. macropholis* (grey bars) individuals for a period of 21 days – each day represents a separate sample.

($F = 8.166$; $df = 2, 6$; $P < 0.05$). The Student-Newman-Keuls test indicated no difference in shelter occupation between *C. polyzonus* and *C. macropholis*, but *C. cataphractus* used significantly fewer shelters than both these species. *Cordylus cataphractus* thus exhibited a higher tendency to aggregate than its congeners.

DISCUSSION

A significant difference was apparent in the pattern of shelter occupation among the three test species. *Cordylus cataphractus* consistently occupied fewer shelters than *C. macropholis* and *C. polyzonus* did under identical experimental conditions. Since this grouping behaviour was additionally exhibited in the presence of an excess of shelter sites, my original hypothesis is rejected for this species: grouping behaviour in *C. cataphractus* is not the result of limited shelter availability. In contrast, *C. macropholis* displayed a pattern of shelter occupation that did not differ significantly from that of *C. polyzonus*. The hypothesis is accepted in this case, in other words, aggregative behaviour among *C. macropholis* lizards is the result of limited shelter availability.

These findings are well supported by field studies. Of 134 *C. cataphractus* collected by Mouton *et al.* (1999) along the western coastal lowlands, 85 % of individuals were found in groups of two or more, illustrating the strong tendency to aggregate in the species. The distribution of *C. cataphractus* is not restricted to these coastal lowlands, where rocky outcrops are limited, but also occur inland and in more mountainous areas, where there is an abundance of crevices. Individuals nevertheless still aggregate in groups in the latter areas (Peers 1930; own observations), indicating mutual attraction of conspecifics. Furthermore, members of a group not only share the crevice as a nighttime refuge, but during daytime the entire group utilizes the rock containing the home crevice as an elevated look-out point from where foraging attempts are launched, despite the fact that this promotes intraspecific food

competition (Mouton *et al.* 2000c). In the case of *C. macropholis*, field studies have shown the incidence of lizards sharing plants to be as high as 89 % (Mouton *et al.* 2000a). Unlike *C. cataphractus*, however, these lizards displayed mutual avoidance when provided with an excess of shelter sites in our experiment. The distribution of *E. caput-medusae* is extremely patchy across the range of *C. macropholis* and the plants can be considered a limited resource, thus forcing lizards to co-inhabit the same plant (own observations). The high incidence of one *C. polyzonus* lizard per shelter in the experiment also correlates with field observations, where individuals are predominantly encountered living solitary (Branch 1998; own observations).

Cordylus cataphractus displays several unique physiological and behavioural characters, which may be associated with energy constraints brought about by the permanent group-living lifestyle of this extreme sit-and-wait forager. These characters include low fecundity, with females giving birth to only one young per year as opposed to two to nine in other cordylids (Flemming unpubl.), an extremely low resting metabolic rate (Mouton *et al.* 2000b), and extremely low activity levels during dry summer months (own observations) when other cordylids remain active. No such adaptations have been encountered in *C. macropholis* as of yet, once again enforcing the hypothesis that aggregative behaviour in *C. macropholis* is the result of limited resource availability.

In light of the evidence that different driving forces are responsible for the grouping behaviour observed in *C. cataphractus* and *C. macropholis*, it becomes questionable whether aggregations of *C. macropholis* should be classified as social groupings. The dense spatial arrangement of *E. caput-medusae* stems allows limited visual contact between individuals and mutual avoidance can easily be maintained. On the other hand, *C. cataphractus* lizards are in constant visual contact and, to a lesser extent, physical contact within their rock crevices (own

observations). Lizards are forced to interact socially and a complex social system is to be expected.

In conclusion, limited crevice availability can be eliminated as being responsible for the strong grouping tendency in *C. cataphractus*. It will be difficult to assess whether the unique characteristics of *C. cataphractus* are the cause of its group-living behaviour or a consequence thereof. In contrast, aggregative behaviour observed in *C. macropholis* appears to be an artifact of limited refuge availability and sociality in this species is potentially not as complex as in *C. cataphractus*. These two species provide ideal opportunities for further investigations into sociality among reptiles.

- CHAPTER 2 -

CHEMOSENSORY EXPLORATION OF CONSPECIFIC SUBSTRATE DEPOSITS IN *CORDYLUS CATAPHRACTUS*

EFFECTIVE individual recognition and intraspecific communication is necessary for cohesive social grouping (Bull *et al.* 2000). Whereas lizards were traditionally considered to be strictly visually oriented animals (Simon 1983), the use of pheromones in chemoreception is now widely recognized as integral to reptilian social behaviour (Mason 1992). Pheromones are defined as chemicals or semio-chemicals produced by one individual that effect a change in the physiology or behaviour of conspecifics (Karlson & Luscher 1959; Cooper & Trauth 1992). Pheromones may provide information on the species (Duvall *et al.* 1980; Simon 1983; Cooper & Vitt 1984), gender and sexual receptiveness (Cole 1966; Cooper *et al.* 1986; Alberts 1992), territorial status (Carpenter 1975; Bissinger & Simon 1979; Gravelle & Simon 1980), social status (Duvall *et al.* 1980; Alberts 1992) kinship (Evans 1959; Duvall *et al.* 1980; Werner *et al.* 1987) and even group affinity (Burghardt *et al.* 1977; Mason 1992; Bull *et al.* 2000) of other lizards. The vomeronasal system is generally accepted to be utilized for such chemoreceptive functions, with the tongue serving as primary sampling device (Graves & Halpern 1989).

Little is known about the extent to which pheromonal communication is used within the African family Cordylidae. Phylogeny plays a major role in the significance of the vomeronasal system (Simon 1983). Of the two major lizard taxa, iguanians rely mainly on their visual capacities for courtship and territorial behaviour (Bissinger & Simon 1979; Cooper 1989), while scleroglossans rely heavily on both vision and chemoreception (Camp 1923). Cordylidae is a scleroglossan family, thus Cooper & Trauth (1992) predicted that cordylids are likely to display a chemoreceptive response akin to that of their closest relatives.

The Jacobson's organ of cordylids resembles that of actively foraging scincids (Malan 1946; Pratt 1948), sister group to the cordylid-gerrhosaurid clade (Lang 1992). Recent studies however emphasize the adaptive nature of chemoreception and its sensitivity to prevailing ecological conditions. This is illustrated by four shifts in foraging mode linked to changes in use of the vomeronasal system for prey chemical discrimination (Cooper 1994). Cordylids are extreme sit-and-wait foragers (Simon 1983; Cooper, 1994). Individuals seldom venture far from their crevices, monitoring the small area around their crevices visually (FitzSimons 1943; Mouton *et al.* 1999; own observations). The tongues of cordylids are scarcely notched (Simon 1983) and the genus displays a tongue-flicking frequency even lower than that of iguanids (Bissinger & Simon 1979). These factors lead Simon (1983) to postulate that chemoreception may be unimportant in Cordylidae, except perhaps during the mating season.

Cooper *et al.* (1996) conducted the first experiment to test pheromonal communication in a cordylid lizard (*Cordylus cordylus*), outside of the mating season. Ceramic tiles were labeled chemically with substrate deposits from individual lizards, and tongue-flicking responses of males and females to these labeled tiles were investigated. Both sexes consistently tongue-flicked more in response to ceramic tiles labeled by conspecifics than to clean tiles. Males tongue-flicked significantly more to male-labeled tiles than either female-labeled or control tiles, with no significant difference in response to the latter two. Females responded significantly more to female stimuli, but male-labeled tiles did not elicit significantly more tongue-flicks than clean tiles. Cooper *et al.* (1994) concluded that *C. cordylus* is capable of pheromonal detection and is able to use it for sex discrimination of conspecific substrate deposits.

Results obtained for *C. cordylus* are unlikely to reflect chemoreceptive abilities of the family as a whole. *Cordylus cordylus* is a solitary living form (Branch 1998; Ruddock *et al.* in press), yet several members of the genus *Platysaurus* are described as gregarious (Branch

1998) and the genus *Cordylus* itself contains at least three species known to display year-round grouping behaviour (Mouton *et al.* 1999). The Australian scincid genus *Egernia* similary contains several gregarious species among which at least one, *E. stokesii* forms stable social aggregations over extensive periods (Main & Bull 1996; Bull *et al.* 2000). *Egernia stokesii* not only recognizes chemical signals of individuals, but individuals can discriminate between pheromones from members of its own group and those of non-group members (Bull *et al.* 2000). As this implies, the ecology and behaviour of social species are likely to influence both the degree to which chemosensory behaviour is utilized, as well as the specific functions for which it is used. My broad objective was to explore the use of pheromonal communication in a group-living cordylid, *Cordylus cataphractus.*

I examined pheromonal communication in *C. cataphractus* by applying methods similar to those used by Cooper *et al.* (1996). The main aims were to establish whether *C. cataphractus* is able to discriminate (1) between conspecific pheromones and neutral controls, and (2) between substrate deposits of conspecific males and females. The secondary aim was to establish whether the observed pattern differed within and outside of the mating season. Results are compared to those obtained for *C. cordylus*. I follow the assumptions of Cooper *et al.* (1996) that individuals leave chemical traces on the substrate and that tongue-flicking is a reliable behavioural index of chemosensory exploration. Chemical signals may be deposited through various exudates, including femoral and generation glandular products (Alberts 1989; Alberts 1991; Van Wyk & Mouton 1992), faeces, urine and skin lipids (Greenberg 1943; Mason 1992). Due to its rupiculous lifestyle, it is hypothesized that *C. cataphractus* will leave chemical traces for social signaling on hard substrates that are visited regularly, regardless of origin or method of deposition (active or passive) of these chemicals. "Tongue-flicking" is used as a general term in this paper, describing either an action where the tongue samples the air, or one where the tongue contacts a substrate or conspecific.

MATERIALS AND METHODS

Two similar experiments were conducted, one within and the other outside of the mating season. For the experiment conducted within the mating season (October – November), 10 males and 12 females (n = 22) were captured; matings were observed in the field at this time of year (own observations). Nine males and eight females (n = 17) were captured on a separate occasion for the experiment conducted outside of the mating season (July – August). Field observations revealed a lack of mating behaviour in *C. cataphractus* at this time of year (own observations).

Study animals were collected at Bergopklip (31° 55' 01" S; 18° 24' 53" E) in the Lambert's Bay district, located on the west coast of South Africa. All specimens were adult lizards, with size at sexual maturity taken as 95 mm (Mouton *et al.* 1999). Males were distinguished from females by the presence of large hemipenal bulges, broad heads, and a relatively large number of generation glands (see Mouton *et al.* 1999). Lizards were transported to and housed at the University of Stellenbosch, and released at their site of capture after completion of the respective two experiments.

Both experiments were conducted as follows. Lizards were housed separately in glass terraria for a 10-day labeling period. Each terrarium contained a shelter site constructed of two ceramic tiles (24.5 x 12 x 1 cm) separated by thin wooden strips. A newspaper substrate was used and the lizards were provided with food (tenebroinid larvae), water ad libitum, and exposure to the natural photoperiod. Room temperature was maintained at 29 °C during the day and followed ambient temperature at night. Lizards spent the nighttime and most of the daytime within the shelters, allowing for sufficient time to label the ceramic tiles chemically.

Trials were conducted in a 2.4 x 3.4 m observation room with a window that allowed exposure to the natural photoperiod and a 1.70 x 0.85 m one-way glass panel that allowed observation with minimum disturbance. A glass terrarium of dimensions 60 x 40 x 28 cm

was used as an unfamiliar test arena. This test arena was washed with water and cleaning agent prior to and between all trials. Fresh newspaper substrate (but no water or food) was provided on each occasion. The two sides of the test cage located at right angles to the observer were covered with cardboard in order to reduce external stimuli.

For each trial, a stimulus tile was inserted into the test cage, touching the side of the cage furthest from the observer. A pre-washed, control tile (hereafter referred to as the "covering tile") was added as a top half to create an entire shelter site and lend a sense of security to the lizards. This was done in light of an earlier experiment where only exposed stimulus tiles were inserted in the test arena. Under these exposed conditions, lizards displayed extremely stressful behaviour by running along the sides of the cage, and never tongue-flicking any stimulus tiles at all.

Lizards were tested for tongue-flicking responses to three consecutive stimuli (using a randomized block design): a male-labeled tile, a female-labeled tile and a control tile prewashed in Alconox and warm water. Since each lizard was exposed to two labeled tiles, only half of the lizards were tested during a first trial run. This prevented use of the same labeled tile for two lizards during trials, which might lead to chemical cross-contamination. All tiles and home cages were washed with water and cleaning agent, a second labeling period ensued, and the remainder of the lizards was tested in a second trial run.

A test lizard was placed in the test arena in front of and facing the shelter site. Care was taken minimizing handling time to reduce stress and prevent defensive tail-biting behaviour. Lizards were observed for 20 minutes, commencing from the first tongue-flick. The number of tongue-flicks touching the stimulus tile, covering tile, substrate, and terrarium glass panels, as well as the number of tongue-flicks sampling the air was recorded. Ambient temperature in the observation room was maintained at 28.1 ± 1.75 °C.

Data Analysis

Due to relative small sample sizes and use of count data, I used nonparametric Friedman's Repeated Measures ANOVA for analysis of differential tongue-flicking responses to stimuli. One Way Repeated Measures ANOVA used only in instances where data sets passed normality (Kolmogorov-Smirnoff) and homogeneity of variance (Levene's) tests and where power of the test exceeded 0.8 ($\alpha = 0.05$ for all tests). Identical procedures were followed to test for significant differences in number of tongue-flicks performed from trial one to trial three (regardless of stimulus type). The Student-Newman-Keuls test was used for performing multiple comparisons. Two sample comparisons were conducted using the Mann-Whitney Rank Sum Test. I also examined whether male-labeled and female-labeled tiles elicited differential responses from male and female lizards by performing 2 x 2 analyses using Fisher exact tests. Data on numbers of tongue-flicks in the text are means ± 1 SE.

RESULTS

General reaction to novel environment

In all cases, release of a lizard was followed by the lizard running into the shelter site directly in front of it. Tongue-flicking of the stimulus and covering tile ensued almost immediately. Only when the lizard was facing directly away from the observer was there any risk of not detecting a tongue-flick. Such occasions were rare, since the lizards predominantly orientated their bodies parallel to the long axis of the shelter. The assumption was made that any tongue-flicks missed in this manner were negligible – all readings were taken by the same observer to ensure consistency. Upon leaving the shelter, lizards continued to explore the remainder of the test arena and rarely returned to the shelter site for the duration of the trial.

Chemosensory exploration within the mating season

In response to the three main stimuli, male lizards tongue-flicked female-labeled tiles the most (6.6 ± 1.9), followed by male-labeled (2.6 ± 0.6), and lastly control tiles (2 ± 0.9) (Figure 2.1). This stimulus effect was not significant (χ^2_F = 3.46, df = 2, $P > 0.1$). In contrast, female lizards performed the greatest number of tongue-flicks when contacting male-labeled tiles (7.4 ± 1.9), tongue-flicked female-labeled tiles second most (6.8 ± 1.3) and control tiles the least (4.2 ± 0.8) (Figure 2.1). Once more none of these differences were statistically significant (χ^2_F = 3.60, df = 2, $P > 0.1$) . The number of males and females which tongue-flicked more in response to male-labeled tiles as opposed to female-labeled tiles, did not differ significantly (Fisher exact, $P = 0.7$), emphasizing the lack of a significant response to main stimuli. There was a non-significant decrease in tongue-flicks elicited from trial one to trial two to trial three (regardless of stimulus type) for lizards of both sexes ($P > 0.1$).

With regard to the entire test arena, males as well as females tongue-flicked predominantly around the shelter site, primarily the covering tile. This difference was statistically highly significant for males ($F = 9.10$; $df = 4$; $P < 0.001$) as determined by One Way RM ANOVA. The cover tile was tongue-flicked significantly more than any other object, including the stimulus tile (Student-Newman-Keuls, $P < 0.05$ for each pair wise comparison). I recorded no other differences in mean tongue-flick rate by male lizards between remaining objects in the test arena. Friedman ANOVA indicates that females responded similarly with differential tongue-flicking responses in the test arena (χ^2_F = 25.33; $df = 4$; $P < 0.001$) of which the most tongue-flicks touched the cover tile ($P < 0.05$). Although there were no difference between number of tongue-flicks touching the stimulus tile and the terrarium glass panels, both of these components were tongue-flicked significantly more than either the substrate ($P < 0.05$) or air ($P < 0.05$), which were explored least of all. In total, females responded to the

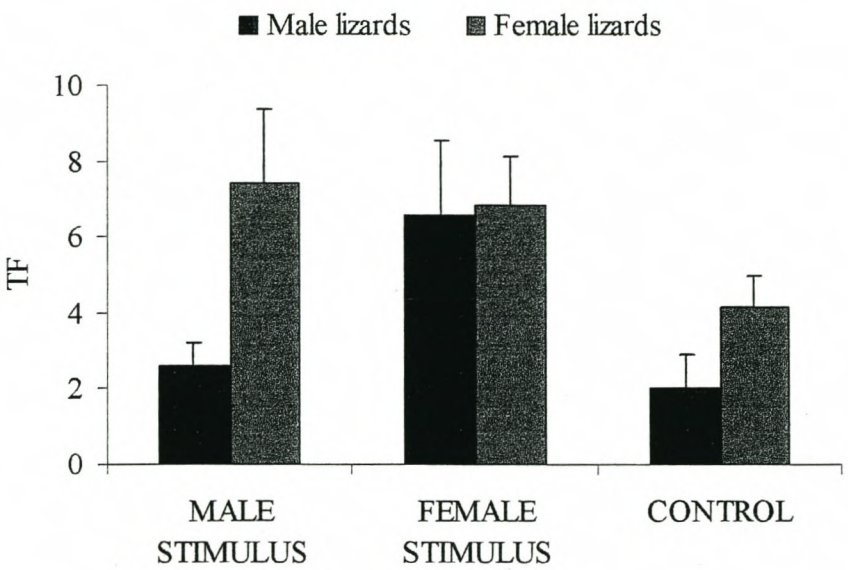

FIGURE 2.1 – Mean number of tongue-flicks (TF) by male and female *Cordylus cataphractus* lizards that touched male-labeled, female-labeled and control tiles within a 20-minute period. Results were obtained during the mating season of *C. cataphractus*. Error bars represent 1.0 SE.

novel test environment with a greater number of tongue-flicks than male lizards (Mann-Whitney, $P = 0.006$).

Chemosensory exploration outside of the mating season

In this instance, both male and female *C. cataphractus* tongue-flicked female-labeled tiles more than male-labeled tiles, with control tiles eliciting the least number of tongue-flicks (Figure 2.2). This stimulus effect was significant for male lizards ($\chi^2_F = 6.79$; $df = 2$; $P = 0.048$). Male lizards tongue-flicked both male-labeled and female-labeled tiles more than control tiles ($P < 0.05$ each), but did not respond differently to the former two. The difference in number of males and females displaying a greater number of tongue-flicks in response to male-labeled tiles as opposed to female-labeled tiles, was not significant at all (Fisher exact, $P = 1.0$). A general decrease was once more apparent in number of tongue-flicks elicited from trial one to trial three. This pattern of habituation was not significant for either sex.

Differential tongue-flicking responses to objects in the entire test arena were once more recorded for both males ($\chi^2_F = 13.18$; $df = 4$; $P < 0.05$) and females ($\chi^2_F = 22.34$; $df = 4$; $P < 0.001$). Males tongue-flicked the air significantly less than any other object in their test environment (Student-Newman-Keuls, $P < 0.05$). No differences were found between any other pair wise comparisons, although the highest mean number of tongue-flicks was again directed at the covering tile. For females, significantly more tongue-flicks were elicited by the covering and stimulus tiles ($P < 0.05$) than any other object, but with no difference recorded within this stimulus pair. Male lizards tongue-flicked both their covering and stimulus tiles significantly less than the females. Once again female lizards tongue-flicked more than male lizards.

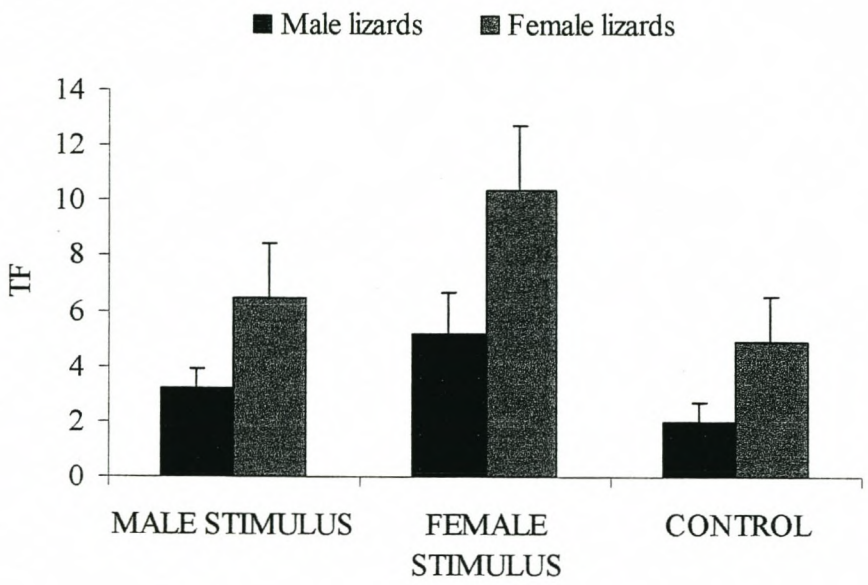

FIGURE 2.2 – Mean number of tongue-flicks (TF) by male and female *Cordylus cataphractus* lizards that touched male-labeled, female-labeled and control tiles within a 20-minute period. Results were obtained outside of the mating season of *C. cataphractus*. Error bars represent 1.0 SE.

Interseasonal comparison of results

The main interseasonal difference was that both male and female lizards tongue-flicked more during the mating season. Males, specifically, tongue-flicked more around the shelter area. This increase in tongue-flicking was however scored for the cover tiles (T = 886.00, n = 27, P = 0.013). Males also tongue-flicked the air (T = 874.50, n = 27, P = 0.023) significantly more during the mating season.

DISCUSSION

Experimental results suggest that *C. cataphractus* could not discriminate between conspecific pheromones deposited on the substrate and blank controls. Although control tiles were tongue-flicked less than male-labeled or female-labeled tiles in all instances, this effect was only marginally significant in one instance (male response outside of the mating season). Furthermore, neither sex was able to discriminate between male and female pheromonal stimuli by means of tongue-flicking behaviour. There was a general tendency for lizards to tongue-flick more in response to stimuli of the opposite sex (except for females outside of the mating season, which displayed a greater response to intrasexual cues), but none of these differences were significant. These findings should be interpreted with caution; non-significant yet positively correlated findings may well be significant at increased sample sizes.

Results differed substantially from those obtained for the congeneric *C. cordylus* in a similar tongue-flicking experiment (Cooper *et al.* 1996). These differential chemoreceptive responses indicate that the vomeronasal system may serve distinct, though not necessarily mutually exclusive, functions among congeneric species. Presence or absence of any chemoreceptive function within each species depends on its relative importance and contribution to inclusive fitness of the individual. This is defined by social and ecological parameters, e.g. type of mating system, degree of territoriality, foraging strategy, and amount

of parental investment. *Cordylus cordylus* not only recognized conspecific cues, but was also able to discriminate between sexes. Males detected and discriminated between pheromones of both sexes, while females were only able to detect same sex pheromones. Individuals showed the greatest response to tiles labeled by the opposite sex, leading Cooper *et al.* (1996) to hypothesize that pheromonal deposits are used for territorial marking in *C. cordylus*. The species is known to be territorial and lizards are highly aggressive to consexuals, especially during the mating season (Burrage 1974; Wirminghaus 1990; Ruddock *et al.* in press). In contrast, *C. cataphractus* is a gregarious form with as few as 15% of adults occurring singly, and social groups may contain several adult males (Mouton *et al.* 1999). Several individuals share a refuge, limited basking space and lookout point for prey (Peers 1930; own observations). Use of chemoreception for territorial marking is superfluous. At such close proximity, visual cues are sufficient for identification purposes and behavioural posturing can convey messages regarding territoriality and social status. With group members crossing the substrate regularly chemical signals would become "clouded", rendering pheromonal discrimination purely by means of substrate deposits improbable.

Cordylus cataphractus consistently tongue-flicked the covering tile more (often significantly so) than any other object in the test arena. It follows logically that volatile components of any pheromonal signal present on the stimulus tile (which is used as the bottom half of each shelter) would be at increased concentrations within the shelter. It has often been postulated that the nasal olfactory system is used for initial detection, localization and identification of the airborne (volatile) components of chemical signals (Alberts & Werner 1993). This, in turn, "switches on" the vomeronasal system for acute discrimination of contact pheromones (non-volatile component) by means of tongue-flicking (Cowles & Phelan 1958; Duvall *et al.* 1980; Simon 1983). This might explain the high number of tongue-flicks recorded and large amount of time lizards spent within the shelter site.

However, lumping the tongue-flick totals recorded for each stimulus tile with those recorded for its corresponding covering tile, had no significant effect on statistical analyses.

Tongue-flicking is apparently utilized in the detection of novel stimuli and for general exploration. A number of lizards display high tongue-flick rates just after emergence, or when placed in unfamiliar areas (Simon 1981). During my study lizards maintained a low tongue-flick rate until placement in the test arena; this lead to an immediate and considerable increase in tongue-flicking behaviour. The slight pattern of habituation that was observed, further supports this hypothesis. Additional support is found in field observations – when *C. cataphractus* individuals encountered novel objects placed by the experimenter around their home crevice, such objects were frequently tongue-flicked (Chapter 4).

In summary, *Cordylus cataphractus* displayed no significantly different tongue-flicking response to male-labeled, female-labeled or control tiles. This was the case in both the breeding and nonbreeding season. This implies a lack of intersexual and intraspecific recognition of substrate deposits for *C. cataphractus*. It is postulated that visual cues are predominantly used for the purposes of intraspecific recognition in this highly social species; the use of chemical communication may be restricted to other functions, such as determination of sexual receptivity.

- CHAPTER 3 -

INTERGROUP MOVEMENTS IN *CORDYLUS CATAPHRACTUS*

KNOWLEDGE of movement patterns of individuals within populations is an important component in studies of both the ecology and evolution of a species (Gregory *et al.* 1987). From an ecological perspective, these demographic processes affect the abundance and distribution of conspecifics, which are key elements in population dynamics (Lidicker 1975; Johnson & Gaines 1990; Kyle & Robertson 1997). Movements are required to avoid inbreeding and access either temporally or spatially heterogeneous resources, thus the nature of dispersal has a marked influence on the spatial ecology of a species (Taylor & Taylor 1977; Pulliam *et al.* 1992). Analysis of movement patterns of individuals is therefore often one of the first steps toward understanding the natural history of a species (Weatherhead *et al.* 1989).

Many factors determine the nature of movement patterns, e.g. age, sex, territory quality, past reproductive success, and social ecology, all of which may produce sex-biased or age-biased dispersal rates (Greenwood 1980; Dobson 1982; Newton & Marquiss 1982; Bensch & Hasselquist 1991). These determining factors are often correlated, rendering it difficult to establish the relative importance of each (Greenwood & Harvey 1982; Pärt & Gustafsson 1989; Newton 1993). Irrespective of the causal factors, movements result in a change of localities, and as such individuals are forced to make multiple habitat choices. Prior habitat selection may well affect habitats chosen later (Switzer 1997a,b). In fact, members of several vertebrate species display a high degree of faithfulness to either a specific site or a group of conspecifics (Greenwood 1980; Switzer 1997b). This in itself has several implications on, for example, sexual selection (Searcy 1979) and population ecology (Villard *et al.* 1995). Although group and site fidelity are well documented among mammal and especially bird species (e.g. Greenwood 1980; Greenwood & Harvey 1982; Switzer 1993),

similar research on reptiles is limited primarily due to the fact that the majority of reptiles lead solitary lives.

The lizard family Cordylidae presents an ideal opportunity for studies on spatial dynamics in reptiles. This family occurs in south Saharan Africa and is comprised of four nominal genera: *Platysaurus*, *Cordylus*, *Pseudocordylus*, and *Chamaesaura* (Loveridge 1944; Lang 1991). While the majority of species are solitary-living forms, several have been described as gregarious, among which the formation of aggregations or groups is often encountered (Broadley 1978; Branch 1998; Mouton *et al.* 1999). Where individuals occur in groups, the nature of conspecific interactions depends on several interacting variables: permanence of the aggregation, dichotomized into temporary and permanent aggregations; the underlying factor responsible for the observed grouping behaviour, whether it is limited availability of resources or adaptation to a state of mutual attraction of conspecifics; and the degree of intraspecific tolerance. Despite the vast array of spatial and social organizations within Cordylidae, surprisingly few attempts have been made to conduct investigations into population ecology and social behaviour within the clade.

The aim of this study was to gather baseline information on short-term intergroup movements in *C. cataphractus*, a cordylid endemic to arid and semi-arid areas along the west coast of South Africa (Mouton 1988). *Cordylus cataphractus* displays the clearest manifestation of permanent grouping behaviour recorded for any lizard to date (Mouton *et al.* 1999). Preliminary experimental research suggests that these aggregations are brought about by mutual conspecific attraction (Chapter 1). Lizards aggregate preferentially when excess food and shelter sites (resources which are limited in the species' natural habitat) are provided. As this implies, a high degree of intraspecific tolerance is present, noticeably among adult males. Groups consisting of more than five members often contain several adult males (Mouton *et al.* 1999).

Group size cannot increase indefinitely, since individual fitness will decline sharply should the carrying capacity of the microhabitat be exceeded. Logic dictates that certain individuals will emigrate from their groups (by choice, or forced by conspecific rivals) to either (1) join separate existing groups, or (2) start new groups in uninhabited refuges. No data are currently available on movement patterns of *C. cataphractus*, with only indirect evidence of its existence. Rocks are often cleared of all inhabiting lizards during specimen collection. Upon inspection of these rocks on subsequent field trips, new lizards are frequently encountered, even in instances where the rocks are situated at a considerable distance from neighbouring groups of lizards (Mouton pers. comm.). *Cordylus cataphractus* is an extreme sit-and-wait forager that undergoes an extensive period of inactivity (Chapter 4). Even during peak activity, in the mating season, lizards are rarely observed to venture further than five meters from their home crevice and individuals spend the majority of their time within 30 cm of the home crevice (Chapter 4). In addition, *C. cataphractus* is sluggish by nature in possessing heavy body armour (Peers 1930). Aforementioned factors have lead many authors to assume that these lizard aggregations represent family units (refer to General Introduction), with intergroup movement presumably restricted to periodic evictions of individuals by rival family members.

I examined intergroup movements by asking the following questions: (1) does intergroup movement exist; (2) which sex and age class display such movements; and (3) in what season (breeding / nonbreeding) do these movements occur. No attempt was made to quantify distances moved by individuals. A mark-recapture was conducted in the natural habitat of *C. cataphractus*. The lizards possess several morphological and behavioural traits that restrict sampling to the collection of individuals from rocks that are small enough to be lifted by crowbar (see Mouton *et al.* 1999). This is an unfortunate bias since intraspecific interactions and resulting movement patterns within large groups will, in all likelihood, differ

from those occurring in smaller groups. I made the assumption that sampling of smaller groups would not affect findings significantly. Larger groups are more likely to display unstable social hierarchies or exceed sustainability of the microhabitat, inducing intergroup movements. If movements occur between smaller groups, results can be extrapolated to larger groups. Where the term dispersal is used it refers to any movement away from an aggregation, including both natal and breeding dispersal (see Southwood 1978).

MATERIALS AND METHODS

The mark-recapture was conducted between March and November 1999 at Bergopklip (31° 55' 01" S; 18° 24' 53" E), located 30 km north of Lambert's Bay on the South African west coast. Several rock koppies (hillocks) are scattered about the sandy coastal plains within which the site is situated. These lowland koppies consist of quartzitic sandstone of the Peninsula Formation (Mouton *et al.* 1999). Loose lying boulders and numerous crevices in larger rock formations provide ideal refuges for groups of *C. cataphractus*. Vegetation is classified as Namaqualand Coastal Belt, a subdivision of Succulent Karoo (Acocks 1988), and is characteristic of low altitude, arid areas. Frequent sea mists reduce aridity along the western coastline.

My study site consisted of a plot of approximately 80 m x 40 m, covering the main body of exposed rocks of a typically "isolated" koppie (the nearest subpopulation of *C. cataphractus* occupied a small ridge ± 700 m away). At least four large rock formations housed groups of 15 plus lizards within inaccessible horizontal fissures. Large freestanding rocks containing *C. cataphractus* groups were equally unsuitable for sampling due to excessive disturbance that would be caused to the microhabitat in the process of removing lizards. Six groups of *C. cataphractus* were easily accessible and were accordingly selected for study. Four of these groups were within 20 m of one another; no other crevices in that

region were occupied by lizards, rendering these four nearest neighbouring groups. The remaining two groups were located approximately 60 m further, at a distance of 7 m from one another. Additional groups were present in the 60 m interval, but within inaccessible crevices. Each study group occupied a single crevice formed by a small to medium sized, freestanding rock resting on either a larger rock base or the ground. Length, width and height of each rock were measured.

Rocks were lifted by crowbar while two helpers assisted in catching lizards by hand. Snout-vent length (SVL) of individuals was measured with calipers to determine age class. Size at sexual maturity is known to be 95 mm for both sexes (Mouton *et al.* 1999). No distinction was made between subadults and juveniles in this study and I will hereafter refer to them collectively as juveniles. Males were distinguished from females by the presence of prominent hemipenal bulges, broad heads, and a relative high number of generation glands (Van Wyk & Mouton 1992).

Each lizard was marked with a unique paint code on its head scales. Codes denoted both individual identity and group membership, which allowed for swift identification during subsequent recaptures. Additional alphanumeric codes were applied with a black marker on the abdominal scales, since it was unknown whether paint codes would wear down on the substrate or whether head scales might be lost during ecdysis. Special care was taken to replace rocks in their original position and to ensure that all lizards returned into their refuges after recapture events. Where individuals displayed the defensive tail-biting behaviour peculiar to *C. cataphractus* (Peers 1930; Mouton *et al.* 1999), tails were manually removed from their mouths before returning such lizards to their crevices.

Members of the six groups were originally marked during March (autumn). Three recaptures were conducted during each of the three consecutive months. This entire period falls outside the mating season of *C. cataphractus* and is also the time they are known to

display the least activity around their home crevices (Chapter 4). A rest period of 90 days was allowed before the next round of recaptures resumed in October, i.e. within the mating season. Once more a total of three recaptures were conducted – early October, late October and mid-November, with each recapture event separated by approximately three weeks.

RESULTS

Initially 27 lizards were captured and marked within the six rock crevices studied. Rocks ranged in size from 0.80 x 0.72 x 0.32 m to 1.65 x 1.75 x 0.45 m. Group size was not linearly correlated with rock size (Spearman Rank Correlation test: $r_s = 0.294$; $P > 0.05$). Group size ranged between three and six individuals. The sex ratio of adult males to adult females was 1 : 1.3 while approximately half of the sample (48 %) consisted of juveniles. Across the entire experimental period a total of 46 lizards (10 males, 15 females and 21 juveniles) were captured within the six groups studied. This represents a sex ratio of 1 : 1.5 adult males to adult females, with the percentage of juveniles decreasing marginally to 46 %. A total of 131 recaptures were obtained from the 46 marked lizards. Forty-one lizards (89.13 % of total) were recaptured at least once, including all 10 males, 13 of the females and 18 of the juveniles. Only six lizards were present in all of the recapture episodes spanning both the mating and the non-mating season. Capture-recapture history is summarized in Table 3.1. Of the 46 lizards encountered, 17 were captured exclusively outside of the mating season and 11 exclusively within the mating season. Thirty-nine percent of the marked lizards were recaptured in both seasons.

Analysis of movements into groups provided the following results (refer to Table 3.2). There was an influx of 19 new lizards into the originally marked sample of 27 lizards. Specifically, 40 % of males, 47 % of females, and 38 % of juveniles handled were not present

TABLE 3.1 - Capture-recapture history of six groups of *Cordylus cataphractus*. The "New captures" column denotes original marks as well as subsequent marking of new individuals entering the six groups. Columns "March" to "Oct. (b)" display recapture counts of marked individuals, indicating the months in which recaptured lizards were first captured (and marked) in. "Oct. (a)" = early October; "Oct. (b)" = late October

		Recaptures of lizards first captured in:						
Date	New captures	March	April	May	June	Oct. (a)	Oct. (b)	*Total captures*
March	27	-	-	-	-	-	-	*27*
April	2	24	-	-	-	-	-	*26*
May	5	23	2	-	-	-	-	*30*
June	1	20	2	4	-	-	-	*27*
October (a)	9	14	0	2	0	-	-	*25*
October (b)	2	16	0	2	0	6	-	*26*
November	0	9	0	1	0	5	1	*16*
Total	***46***	***106***	***4***	***9***	***0***	***11***	***1***	***177***

TABLE 3.2 – Summary of movements of *Cordylus cataphractus* individuals into and out of the six study groups, both within and outside of the mating season. The last column represents the total number provided in each row as a percentage of the subset of lizards concerned

		Outside mating season	Within mating season	*Total number*	Percentage of grand total caught
Number of **unmarked** lizards entering groups	Males	2	2	*4*	40
	Females	1	6	*7*	47
	Juveniles	5	3	8	38
	Total	*8*	*11*	*19*	
Number of **marked** lizards entering groups	Males	1	1	*2*	20
	Females	1	3	*4*	26
	Juveniles	0	1	*1*	5
	Total	*2*	*5*	*7*	
Number of **marked** lizards that left groups	Males	4	3	*7*	70
	Females	2	8	*10*	66
	Juveniles	4	13	*17*	81
	Total	*10*	*24*	*34*	

during the original capture. These new recruits entered the experimental groups both within and outside of the mating season. Furthermore, of seven marked lizards that had left their respective groups, six returned to their original groups and one was recaptured in its neighbouring group. An equal number of male lizards (marked or unmarked) entered the experimental groups both within and outside of the mating season. In contrast, more females (marked or unmarked) entered the groups during the breeding season than during the nonbreeding season, although this difference was not statistically significant if equal numbers were to be expected ($\chi^2 = 2.28$; $P > 0.05$).

Thirty-four marked lizards were absent during subsequent recaptures (refer to Table 3.2). Juveniles displayed the highest rate of movement out of groups, with 81 % of all juveniles encountered leaving their groups on at least one occasion. In comparison, 70 % of males and 66 % of females left their groups at least once (refer to Table 3.2). In every category only one individual left the same group twice.

DISCUSSION

Cordylus cataphractus displayed a greater degree of intergroup movement than would be expected if groups represent family units, as is commonly assumed (Peers 1930; Branch 1998). Monitoring of *C. cataphractus* groups in their natural habitat revealed a high percentage influx of new lizards into established groups, coupled with large numbers of lizards leaving groups. These movements were recorded for adult males, adult females, as well as juveniles, and occurred both outside of and within the mating season.

Despite a high recapture rate of 89 %, only 39 % of marked lizards were recaptured in both seasons. Counts of events where marked lizards left their groups were not regarded as reliable measures of dispersal. This precautionary assumption was made in light of the high percentages of lizards that left their groups - such high mobility is likely to be an artifact of

microhabitat disturbance, although to an unknown extent. Lizard movements into the experimental groups were more suitable as a measure of dispersal, since such moves occurred independent of any artificial disturbance.

Unmarked lizards entered the groups both within and outside of the mating season, an unexpected result considering the low activity levels recorded for this species outside of its mating season (Chapter 4). The influx of lizards furthermore includes not only males, but also females and juveniles. This contradicts the prediction of Mouton *et al.* (1999) that minimal female dispersal and delayed juvenile dispersal are benefits gained from the species group-living nature. The evolution of increased dispersal rates is however often selected for in temporally variable habitats, such as this (Johnson & Gaines 1990). It was not possible to infer whether sex-biased dispersal was present. That would require knowledge of the operational sex ratio of the entire surrounding population from which new recruits may be gained, in order to calculate the expected ratio of unmarked males to unmarked females entering groups. This poses a problem - composition of *C. cataphractus* groups differs markedly between small and large groups sizes, yet it is often impossible to extract large groups from rock fissures without inflicting serious damage to the habitat. Larger groups contain relatively more male lizards and thus skew the sex ratio towards males (Mouton *et al.* 1999). The sex ratios obtained in this study are all in favour of females, indicative of the small groups sampled. The difference in sex ratios between the original and total captures furthermore illustrates the variability introduced by surrounding groups of different size classes.

- CHAPTER 4 -

THE EFFECT OF GROUP SIZE ON SEASONAL PATTERNS OF ACTIVITY AND FORAGING IN *CORDYLUS CATAPHRACTUS*

PROXIMATE environmental fluctuations have a considerable influence on the life-history parameters and demographic traits of lizards. The temperature regime determines potential activity times required for foraging, basking, social interactions and other activities (Grant & Dunham 1985; Peterson *et al.* 1993). Secondly, variation in precipitation is directly responsible for shifts in food availability, which is linked to parameters such as growth rate, reproduction and survivorship (Abts 1987; Smith *et al.* 1995). Consequently these two climatic variables limit the resources available for partitioning under competitive and predatory pressures.

The first objective of this study was to describe seasonal patterns of activity, with an emphasis on foraging activity, in the armadillo girdled lizard, *Cordylus cataphractus*. This rupicolous cordylid is endemic to the South African west coast (Mouton 1988; Branch 1998), a semi-arid region where both climate and habitat are temporally highly variable. Long periods of drought are a common occurrence, despite the cooling effect of frequent sea mists along the coastline. The second objective was to examine the effect of group size on the aforementioned activity patterns. Whereas seasonal aggregations are not uncommon among lizards (e.g., Worthington & Sabath 1966; Powell *et al.* 1977; Ruby 1977; Graves & Duvall 1995), the permanent grouping behaviour displayed by *C. cataphractus* is a rare phenomenon. A number of species in the Australian scincid genus *Egernia* have been reported to live in communal aggregations (Hutchinson 1993; Bonnett 1999; Duffield & Bull 2001). Most species in the African cordylid genus *Platysaurus* are also described as gregarious (Broadley 1978; Branch 1998), but little detailed information is available on either of these genera. Of

three *Cordylus* species known to display permanent grouping behaviour, that of *C. cataphractus* is the most distinct and groups of up to 30 individuals are regularly encountered (Mouton *et al.* 1999).

The benefits of group living among lizards, if any, are not well understood. As of yet, no quantitative data exist to back up proposed hypotheses such as increased vigilance, delayed dispersal of juveniles and parental care (e.g., Peers 1930; Mouton *et al.* 1999). In fact, the costs of group living are more universal and include competition for resources, increased transmission of parasites, increased visibility to predators, infanticide and inbreeding depression (Alexander 1974; McRae 1996; Connell 2000; Davis & Brown 2000). Unlike the Australian *Egernia* species, which are herbivores, *C. cataphractus* is insectivorous and an extreme sit-and-wait forager (Mouton *et al.* 2000b). Coupled with the temporal food constraints associated with a drought-prone region, it is safe to assume that *C. cataphractus* group members experience strict intraspecific competition for prey items. In their analysis of the diet of this species, Mouton *et al.* (2000c) indeed found that a significantly higher proportion of group-living individuals had empty stomachs than solitary living ones. In addition to climatic factors, group size therefore has the potential to be a key determinant in the activity regime of *C. cataphractus*. The following hypotheses regarding activity patterns and foraging ecology are considered:

(1) *Cordylus cataphractus* displays selective inactivity. According to one theory, it is adaptive for lizards to be active whenever the weather permits, because activity provides the opportunity for thermoregulation, feeding, reproduction and territorial defense (Huey 1982). A counter-argument states that there might well be a selective advantage to inactivity. Inactivity can increase survivorship by reduced predation risk, water and energy conservation, or reduced temporal overlap of conspecifics dependent upon similar resources (Simon & Middendorf 1976; Rose 1981; Huey 1982). Such advantages would clearly benefit a group-

living species such as *C. cataphractus*. (2) Activity peaks in springtime, following winter rainfall. During this time prey availability is presumably higher and intraspecific food competition among group members accordingly at its lowest. Food is readily available to provide sufficient energy for springtime mating. (3) There are less potential prey captures per lizard in larger groups. (4) There are relatively more competitive encounters for prey items in larger groups. (5) Lizards in larger groups perch further from their crevice. (6) Individuals in larger groups run further to catch prey. Competition levels are hypothesized to decline with increasing distance from the home crevice, as predation risk increases accordingly. (7) Lizards go on sporadic lengthy foraging excursions. This would increase the chance of a successful prey capture attempt. This hypothesis was formulated in view of the heavy armour and peculiar tail-biting behaviour of *C. cataphractus*, which are defensive strategies associated with open areas. (8) Lizards in larger groups are active over longer periods per day, due to higher levels of food competition and the resultant lower energy gain per unit time.

The term activity is used in its broadest sense in this study (*sensu* Foà *et al.* 1992) with the total number of lizards observed per unit time serving as an index of activity. An "active" lizard is defined as any lizard that can be visually detected outside of its crevice, including immobile lizards. In this sense, activity includes a repertoire of behaviours, e.g. foraging, sexual and competitive interactions, basking, and thermoregulatory shuttling (Foà *et al.* 1992). The obvious limitation to this definition, especially considering the group-living nature of *C. cataphractus*, is that lizards inside the crevice are not necessarily "inactive", particularly during daytime. I have nevertheless used this definition, considering that it is a common parameter in studies of activity cycles of lizards and due to the confounding factors associated with attempts at observing refuge activity.

MATERIALS AND METHODS

Study area

The study site is located at Bergopklip (31° 55' 01'' S; 18° 24' 53'' E), 30 km north of Lambert's Bay, South Africa, where dense colonies of *C. cataphractus* occur in scattered rocky outcrops on the coastal plains. Sandstone formations, consisting of quartzitic sandstone of the Peninsula Formation (Mouton *et al.* 1999), provide an abundance of suitable crevices for this rupicolous species. Surrounding vegetation is classified as Namaqualand Coastal Belt, a subdivision of Succulent Karoo (Acocks 1988), and is characterized by a variety of mesembs. The climate is arid with an annual rainfall below 200 mm, consisting mainly of winter rains. Regular sea mists, however, reduce aridity to a great extent (Mouton *et al.* 1999).

Study groups and observational periods

Three *C. cataphractus* groups of different sizes were chosen for study: a small group (6 members), a medium-sized group (17 members) and a large group (27 members). The rock inhabited by each group was required to be loose standing with a simple crevice. This avoided potential confusion of group membership caused by neighbouring groups inhabiting complex crevices in large rock assemblages. Care was taken to choose rocks that contain a crevice that (1) was easily observable through telescope from a distance of approximately 50 m, and (2) permitted observations from the opposite side of the rock through binoculars at a distance of approximately 40 m. This allowed two observers to collect data simultaneously from elevated vantage points on opposite sides of the rock, maximizing the field of visibility. Preliminary focal counts established approximate group sizes within suitable rocks, verified during the first round of observations. In order to avoid microhabitat disturbance and stress-related behaviour by the lizards, no attempt was made to mark individual lizards. All three

groups were located within 200 m of one another to reduce variability in microclimate. The following data were collected for each of the three rocks: length, width, height, slope of the crevice, and the direction that the crevice faced.

Field observations were conducted between September 1998 and October 1999, during the following three seasons: February–April (autumn), May–July (winter), and August–October (spring). During each period, a minimum of three observational days was allocated per group. Particular care was given to include at least two days with similar weather conditions, namely, sunny days with little cloud cover or wind.

Meteorological data

Prior to April 1999, light intensity and temperature were recorded with an MCS 120-02W Data logger (data read with MCS 430 Reader Version 1.62) and subsequently with Hobo H8 Family data loggers (data read using BoxCar Pro Version 3.51 for Windows). Loggers were positioned and activated on the day prior to commencement of observations and removed at termination of observations, always at times when no lizards were active. The loggers were set to take readings at 30-minute intervals. Two temperature probes were utilized to measure crevice temperature and rock surface temperature respectively. Rainfall and additional temperature data were obtained from the Nortier weather station (Clanwilliam district: 32° 02' S; 18° 20 ' E; altitude 98 m), 12 km south of the study site.

Observational procedure

Observations commenced at 08:00 and continued until activity ceased in the late afternoon or, in a few instances, until it became too dark to distinguish lizard activity through the telescope. Recordings of activity were made at 30-minute intervals (coinciding with data logger recordings and weather observations) by two observers from opposite vantage points.

The total number of lizards outside the crevice was counted and each lizard's approximate position in relation to its home crevice was plotted on a pre-drawn map of the rock and surrounding area. To aid with distance estimations, small crosses were drawn with permanent marker on the rock surface at 10 cm and 30 cm intervals from the crevice respectively. Adjacent markings were 60 cm apart. One or two lizards initially tongue-flicked these marks on passing them, but otherwise appeared undisturbed by their presence. Small stones, gathered in the vicinity, were used as 1 m markers on the sand substrate.

On each foraging attempt, the following data were recorded on dictaphone: (1) date and time; (2) the lizard's distance from its crevice, prior to launching the prey capture attempt; (3) the straight-line distance run by the lizard to the point where the prey was captured, or to where the lizard turned around during unsuccessful attempts; (4) whether the prey capture event was successful or unsuccessful; (5) the number of competitive events, i.e., when a second lizard competed for the prey item. After all lizards had retreated into the crevice in the evenings, lizard trails were measured in the loose soil surrounding their home rock. Measurements were taken for trails exceeding the 0.3 m mark only and were compared with dictaphone data to eliminate duplication. The sand was leveled out each evening and checked for fresh tracks each morning before onset of daily observations.

Data were tested for normality and homogeneity of variance using Lillifors and Levene's test respectively. One Way ANOVA tests were used to determine the significance of differences among means, followed post hoc by Scheffé's test for multiple comparisons. Alpha = 0.05 in all tests.

RESULTS

Monthly rainfall figures are provided in Figure 4.1, and monthly mean minimum and mean maximum ambient temperatures in Figure 4.2. During 1999, the study area received 210 mm rain. Rain was virtually absent during autumn (February to April) while mean maximum temperatures peaked, with a high of 40.7 °C. Rainfall mainly occurred during late winter / early spring (July to September) in this particular year, coinciding with the lowest recorded mean monthly temperatures. Dimensions of the rocks inhabited by the three study groups are summarized in Table 4.1. Group size was not linearly correlated with home rock size (Spearman Rank Order test: $r_s = 0.292$; $P > 0.50$).

Activity patterns of the large group

Very low levels of activity were recorded in this group during autumn. No more than seven lizards were observed at any given time (Figure 4.3). Activity occurred from 09:30 until after 20:00. The maximum number of lizards was in fact often recorded in the last light of day after sunset (19:35), which is not apparent in Figure 4.3 since these counts were obtained between 30-minute scans. The pattern of activity approached bimodality on all three days during autumn. Active lizards were primarily located within 1 – 10 cm from the crevice opening, with only a small proportion venturing into the 11 – 30 cm distance interval (Figure 4.4). No lizard was ever observed to engage in social or foraging activity during this time of year. Maximum rock temperature (T_{Rmax}) was 48.16 °C and maximum crevice temperature (T_{Cmax}) 32.62 °C.

No lizards were observed outside their crevice on sunny days during winter (T_{Rmax} = 27.52 °C and T_{Cmax} = 24.01 °C) . A single lizard was noticed once on a cloudy day during this period, emerging briefly between 14:00 and 14:30.

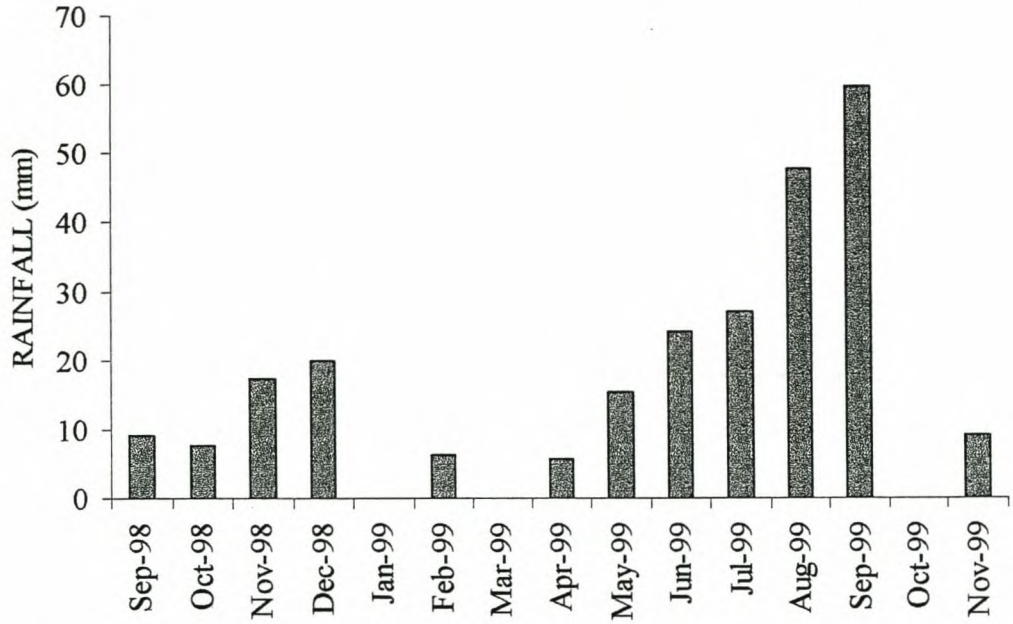

FIGURE 4.1 – Total monthly rainfall figures (mm) recorded in the study area.

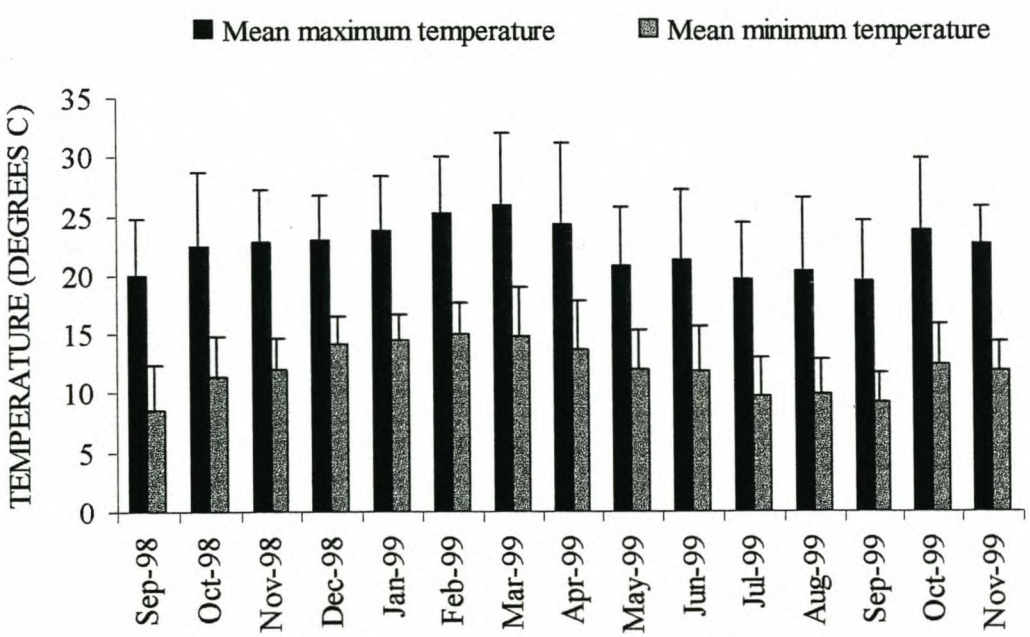

FIGURE 4.2 – Mean minimum and mean maximum ambient temperatures (°C) recorded in the study area.

TABLE 4.1 – Dimensions of the three rocks, inhabited respectively by a large (n = 27), medium-sized (n = 17) and small (n = 6) group of *Cordylus cataphractus* lizards. "Crevice direction" denotes the compass point that the crevice faces, and "Slope" is the angle of the crevice opening from the horizontal plane.

	Rock dimensions				
	Length (m)	Width (m)	Height (m)	Crevice direction	Slope (degrees)
Small group	2.17	1.06	0.40	NE	20
Medium-sized group	3.25	2.72	0.45	W / E	90
Large group	3.50	1.30	0.55	SW	25

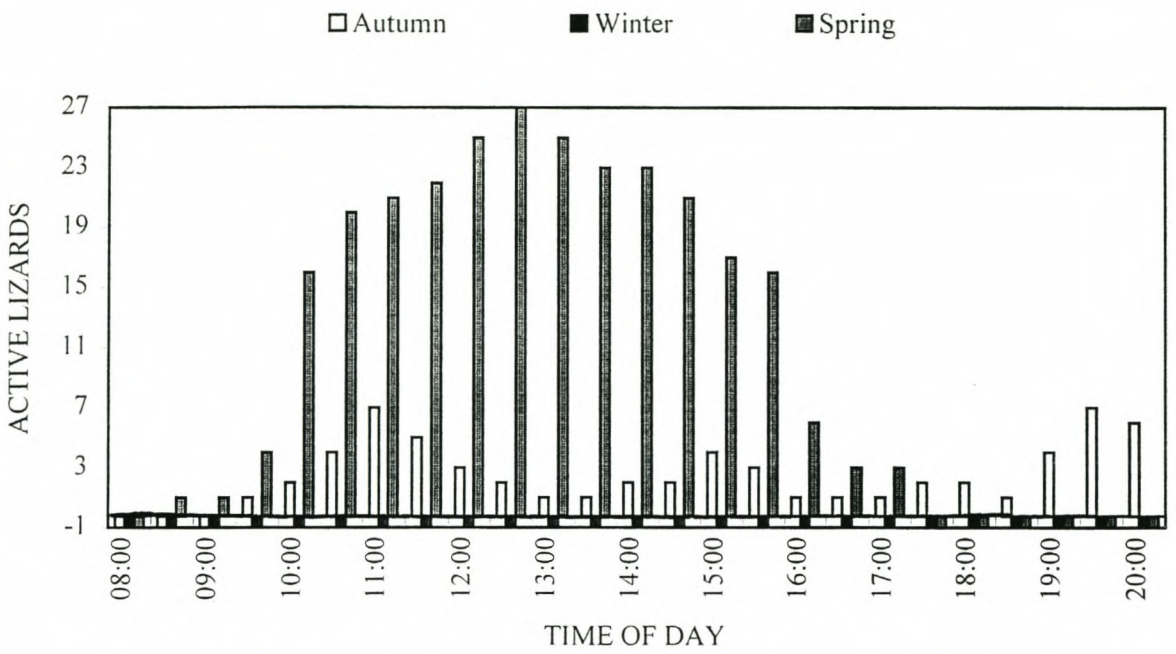

FIGURE 4.3 – Average diel activity patterns across three seasons in a large group of *Cordylus cataphractus* lizards (n = 27). Low, approximately bimodal activity occurs during autumn (clear bars). Lizards become completely inactive during winter (solid bars), and a high level of unimodal activity is present in spring (grey bars). Active lizards are defined as the number of lizards visible outside of the crevice. Sub-zero bars on the graph display inactivity.

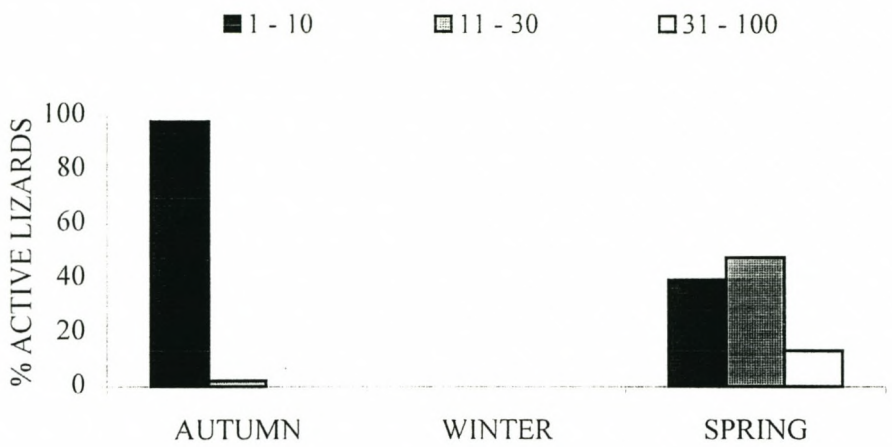

FIGURE 4.4 – Average seasonal variation in spatial use by active *Cordylus cataphractus* lizards of the large sized group (n = 27). Bars represent the proportion of active lizards (independent of the total number of lizards counted) recorded at various distance intervals from the refuge, namely, 1 – 10 cm, 11 – 30 cm, and 31 – 100 cm. No lizards were observed further than 100 cm from the respective crevices.

This group displayed its highest activity levels during springtime (Figure 4.3). Lizards were observed between 08:30 and 17:00, with a distinct unimodal pattern of activity on all three days (T_{Rmax} = 29.76 °C and T_{Cmax} = 19.84 °C). Activity peaked at noontime and lizards returned into the crevice before sunset (18:50). Although 40 % of lizard counts were still obtained in the 1 – 10 cm distance interval, the majority was recorded between 11 and 30 cm from the crevice, contrary to the situation in autumn. A small number of individuals even ventured as far as 31 – 100 cm from the crevice (Figure 4.4). Social interactions were abundant with high frequencies of head-bobbing, strutting, tail-sweeping, and biting. Foraging activity was similarly prolific during this period.

Activity patterns of the medium-sized group

During three days of observations in autumn, no active lizards were recorded (T_{Rmax} = 39.60 °C and T_{Cmax} = 28.00 °C) (Figure 4.5). During winter, activity outside the crevice was once again virtually non-existent. Only a single lizard emerged briefly at noon one day, but did not venture further than 10 cm from its crevice (T_{Rmax} = 37.70 °C and T_{Cmax} = 25.56 °C). Prolific activity was observed during spring. A predominantly unimodal activity pattern shifted to bimodality on excessively warm days (T_{Rmax} = 41.99 °C and T_{Cmax} = 29.90 °C), thus averaging of data produced the multimodal curve apparent in Figure 4.5. Lizards were observed between 08:30 and 19:00, returning to their crevice before sunset. Activity was mainly restricted to within 10 cm of the crevice, although lizards moved as far as the 30 – 100 cm distance interval (Figure 4.6). Social interactions were abundant and foraging excursions were frequent.

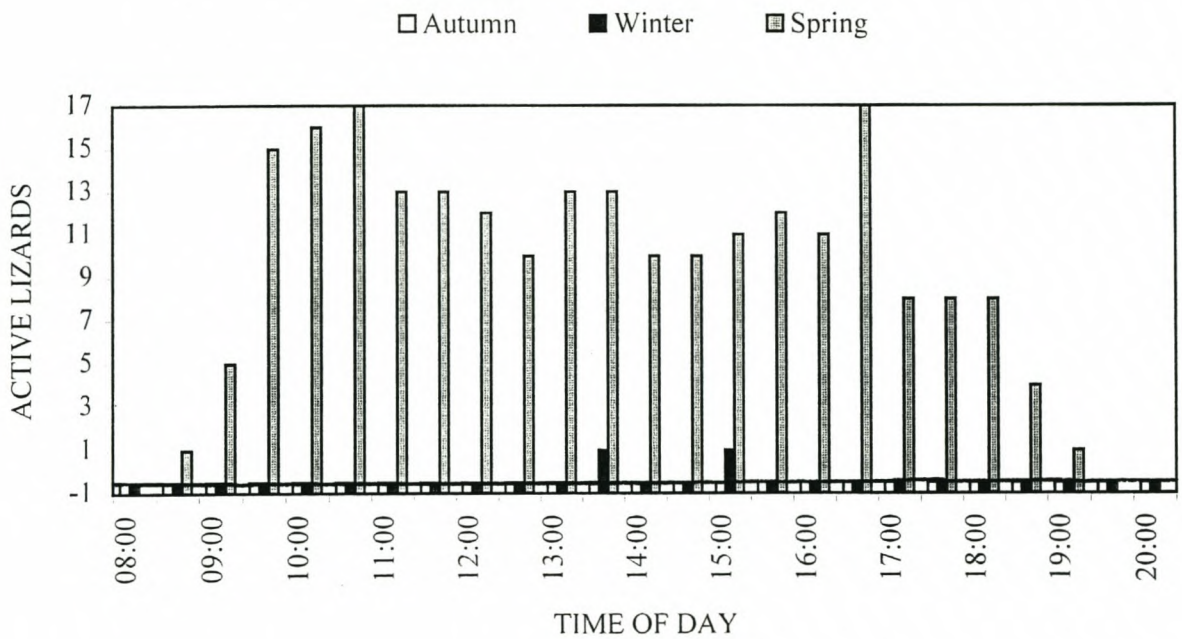

FIGURE 4.5 – Average diel activity patterns across three seasons in a medium-sized group of *Cordylus cataphractus* lizards (n = 17). No activity was observed during autumn (clear bars) and lizards were mainly still inactive during winter (solid bars). In spring, however, high levels of activity were present (grey bars). Active lizards are defined as the number of lizards visible outside of the crevice. Sub-zero bars on the graph display inactivity.

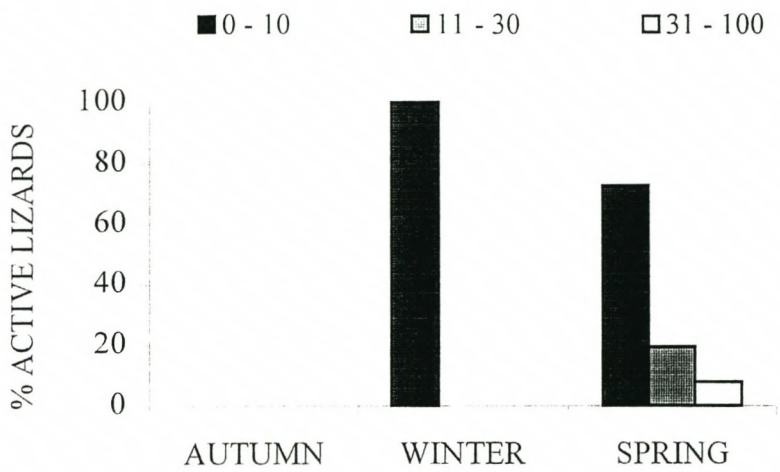

FIGURE 4.6 – Average seasonal variation in spatial use by active *Cordylus cataphractus* lizards of the medium-sized group (n = 17). Bars represent the proportion of active lizards (independent of the total of lizards counted) recorded at various distance intervals from their refuge, namely, 1 – 10 cm, 11 – 30 cm, and 31 – 100 cm. No lizards were observed further than 100 cm from the respective crevices.

Activity patterns of the small group

This was the only group in which individuals emerged from the crevice throughout the year. During autumn, activity occurred from 11:00 until after 20:00 (Figure 4.7), when light conditions deteriorated and prevented further observation. A distinct unimodal pattern of activity was present, peaking in the late afternoon just before sunset (T_{Rmax} = 37.94 °C and T_{Cmax} = 33.02 °C). No lizards moved beyond 10 cm of the crevice opening, and no foraging or social activity was recorded.

During winter, observation days commenced on the first day following the first decent rainfall event. Foraging attempts were abundant as the lizards responded to an explosion of insect life. A unimodal activity pattern was still present, but peaked earlier in the day (Figure 4.7). Lizards were only observed between 10:30 and 17:30 (T_{Rmax} = 34.85 °C and T_{Cmax} = 31.12 °C). Although lizards primarily remained within 10 cm of the crevice, some time was spent in the 11 – 30 cm interval and a small fraction within the 31 – 100 cm interval (Figure 4.8). Minimal social interactions occurred.

During spring a definite bimodal activity pattern was assumed (Figure 4.7). Active lizards were observed between 08:00 and 18:30 with much early morning activity (T_{Rmax} = 41.99 °C and T_{Cmax} = 34.43 °C). The majority of time was still spent within 10 cm of the crevice, but with increased proportions of activity in the 11 – 30 cm and 31 – 100 cm distance intervals as opposed to the pattern observed in winter.

Foraging data

A distinct seasonal pattern of foraging activity emerged. This seasonal effect was highly significant across all three study groups ($F = 57.67$; $df = 2, 19$; $P < 0.001$). There was also a highly significant group size effect ($F = 26.33$; $df = 2, 19$; $P < 0.001$) with significant interaction between season and group size ($F = 9.07$; $df = 4, 19$; $P = 0.003$). No foraging

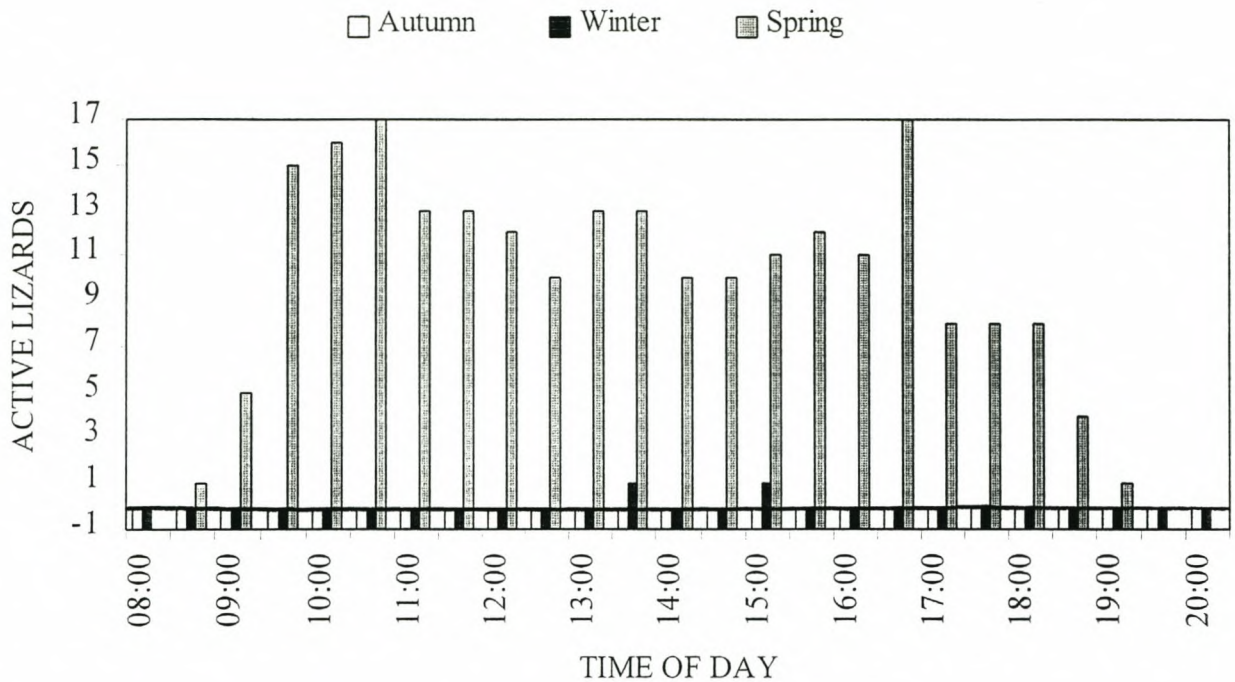

FIGURE 4.7 – Average diel activity patterns across three seasons in a small-sized group of *Cordylus cataphractus* lizards (n = 6). Activity was observed in all seasons but still peaked in spring (grey bars). During autumn (clear bars) and winter (solid bars) activity was unimodal, switching to bimodality in springtime (grey bars). Active lizards are defined as the number of lizards visible outside of the crevice. Sub-zero bars on the graph display inactivity.

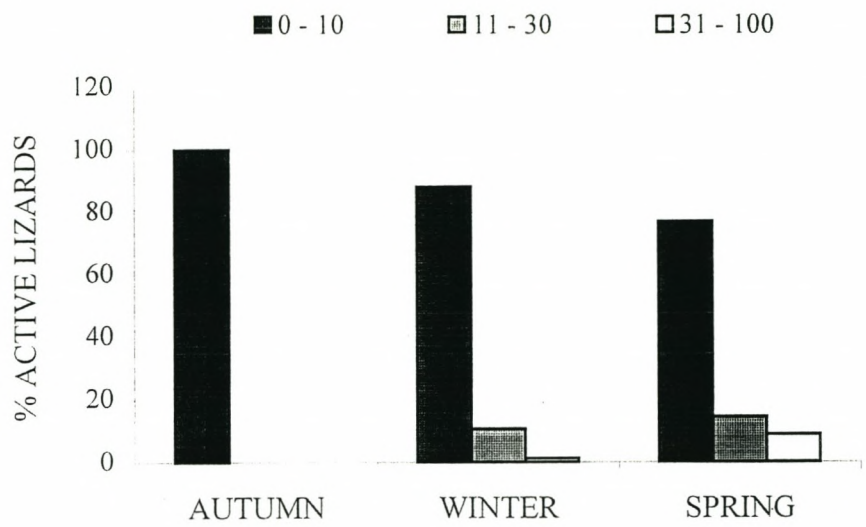

FIGURE 4.8 – Average seasonal variation in spatial use by active *Cordylus cataphractus* lizards of the small-sized group (n = 7). Bars represent the proportion of active lizards (independent of the total of lizards counted) recorded at various distance intervals from their refuge, namely, 1 – 10 cm, 11 – 30 cm, and 31 – 100 cm. No lizards were observed further than 100 cm of the respective crevices.

attempts were observed in either the large, medium-sized or small group during autumn. This was despite the fact that some lizards from the large group and most members of the small group were observed outside their respective crevices. Temperatures reached a high and virtually no rainfall occurred at this time of year (Figure 4.2). During winter ambient air temperatures reached a low, while rainfall steadily increased (Figure 4.1). Foraging attempts were still absent in the large and medium-sized groups, although no lizards were observed outside of the crevice at this stage. In late winter, lizards of the small group were active and 24 foraging attempts were recorded across three days. (In this instance, observational days followed directly after a rainfall event – brief visits to the other two groups revealed that their members also emerged at this stage.) All three groups displayed prolific foraging activity in springtime, which was significantly higher than recorded in the previous seasons (Scheffé's test: $P < 0.05$). Ambient air temperatures started to rise and rainfall passes its peak (Figures 4.1 and 4.2). Since foraging activity was mainly restricted to this time of year, all subsequent analyses are relevant to this season only.

The mean number of foraging attempts observed per day was 49 for the large group, 18 for the medium-sized group, and 23 for the small group. Figures obtained for separate days were divided by the number of members per group; this provided an estimate of the potential prey capture events available per individual. Using these figures, ANOVA indicated that there was a significant difference in prey capture opportunities per lizard for different group sizes ($F = 31.23$; $df = 2$; $P = 0.004$). Scheffé's test isolated the small group as possessing more prey capture opportunities per lizard than both the large and medium-sized groups, with no difference between the latter two. A total of 14 competitive events for prey items were witnessed in the large group, three such events in the medium-sized group, and four in the small group. After adjusting these figures for group size, however, this did not represent a proportionate difference in the number of competitive encounters between groups.

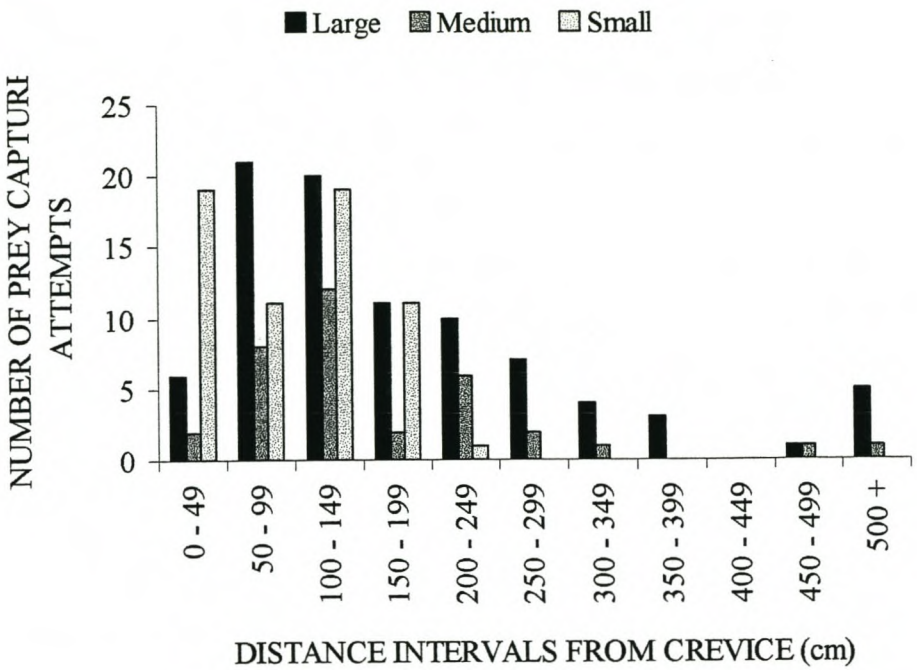

FIGURE 4.9 – Frequency histogram depicting the number of foraging attempts (y-axis) observed at increasing distance intervals (x-axis) from the home crevice. Solid bars represent foraging attempts by *Cordylus cataphractus* individuals from the large group, grey bars denote attempts by members from the medium-sized group, and clear bars indicate attempts by lizards from the small group.

Analysis of the distances run to catch prey revealed a significant group size effect (F = 6.057; df = 2; P = 0.003). Lizards in the small group ran significantly smaller distances to capture prey successfully than lizards in both the large and medium-sized groups ($P < 0.05$). A graph of prey capture events at respective distance intervals from the crevice (Figure 5.1) renders approximately parabolic trends, skewed to the right, in all three groups. The majority of prey capture attempts terminated between 50 and 100 cm from the crevice, with a gradual decline thereafter. A number of outliers (500 cm plus) were only observed in the medium-sized and large groups. The maximum distances run by lizards in the large and medium-sized group to catch prey were 20 m and 5.72 m respectively.

DISCUSSION

Activity patterns of *Cordylus cataphractus* were closely linked with the main climatic variables, temperature and rainfall. As hypothesized, activity of all three groups studied (though more pronounced in the larger two), was basically restricted to springtime, coinciding with the mating season. This was the only time during which social interactions were observed. Following the first decent rainfall event, a pulse of insect life allowed lizards to forage prolifically. Low ambient temperatures furthermore prevented loss of energy through heightened metabolism. For the remainder of the year, activity virtually ceased. When lizards did occasionally emerge, most noticeably in the small group, they did not venture further than 10 cm from the crevice and displayed no foraging or social activity. This stands in sharp contrast to solitary-living, sympatric species such as *C. polyzonus*; individuals of the latter species, living in close proximity to the *C. cataphractus* groups, were observed to forage throughout the year, running far from the crevice if necessary (pers. obs.). This confirms the hypothesis that *C. cataphractus* displays selective inactivity, and suggests that it may be a survival strategy related to group-living behaviour. Schoener (1977) states that reptiles do not

gain from feeding during relatively unfavourable periods and will specialize by feeding during particularly favourable times - foraging ensues when net energy (either gain or loss) is higher than the potential loss while inactive. It is thus hypothesized that the additional energetic costs associated with heightened competitive levels in a group set-up renders emergence too costly for *C. cataphractus* individuals during the warm, dry months.

Such selective inactivity necessitates sufficient build up of energy reserves during the wet season. Flemming & Mouton (unpublished data) found that *C. cataphractus* develops exceptionally large fat bodies, more than three times larger than those recorded for any other cordylid. These observations were made during October, which, for all practical purposes, can still be considered as part of the wet season. Moreover, Mouton *et al.* (2000b) recorded exceptionally low resting metabolic rates with some degree of thermal independence for this species, further reducing energy expenditure during the warm, dry summer months. Conversely, a low metabolic rate will act as constraint during the wet season when a fast rate of energy conversion is required. This aspect requires further investigation.

Cordylus cataphractus, like most other members in the genus, has a prenuptial reproductive cycle with spermatogenesis peaking in males at the time of ovulation in females (Flemming & Mouton, unpublished data). Matings and mating attempts were indeed observed in both September and October (pers. obs.), coinciding with the period of peak foraging activity. It appears that the species cannot afford the additional energy burden that would result from temporal separation of foraging and mating activity. *Cordylus cataphractus* does not occur in summer rainfall areas, where such separation may be requisite, and is restricted to winter rainfall areas in the west. Moreover, the species does not occur in the high rainfall areas to the south, where there is potentially a lack of sufficient clear, sunny days for individuals to emerge and replenish energy reserves for the dry period.

The family Cordylidae is considered to be a cool-adapted group of lizards as indicated by their viviparous reproductive mode (excluding *Platysaurus*), rupicolous lifestyle and sit-and-wait foraging strategy (Mouton and Van Wyk 1997). Taxa with lower preferred body temperatures usually occur in cooler climates, possess low heat tolerance, and display bimodal activity on sunny days (Heatwole *et al.* 1969; Schoener 1970). In contrast, those species with a higher preferred body temperature display unimodal activity on sunny days. Within the genus *Cordylus*, bimodal activity has been recorded for three species and is attributed to lower preferred body temperatures that allow occupation of cooler habitats (Cronjé, unpublished). Although activity levels were low, the large group displayed a bimodal pattern during autumn, and the medium sized and small groups a similar pattern during spring. In general, the activity patterns recorded for *C. cataphractus* thus reflect the cool-adapted nature of the family. Losos and Mouton (unpublished data) recorded activity body temperatures for this species similar to that for other cordylids. A unimodal pattern was, however, recorded for the large group during September, but environmental temperatures were considerably lower than during October when a bimodal pattern was recorded for the other groups. Shifts between uni- and bimodality are not uncommon in temperate zone lizards (Schoener 1970).

Assuming that distribution of food resources is fairly homogenous, the higher number of individuals in large groups implies that each lizard will have fewer potential opportunities to forage. This is supported by an analysis of observed counts of foraging attempts, adjusted for group size. It did not, as hypothesized, lead to a proportionate increase in agonistic encounters via intragroup rivalry for food items in larger groups. Such interference competition is presumably energetically too costly in a group-living scenario. As alternative, lizards from larger groups perched significantly further from the crevice and ran significantly further to catch prey in relation to conspecifics in a small group. Sporadic lengthy foraging

excursions, in excess of five meters and reaching a maximum of 20 m, were also present in the larger two groups studied. This may account for the heavy armour and tail-biting behaviour in *C. cataphractus*. Such defense mechanisms are of little use within a crevice.

The larger two groups, where intraspecific food competition is more stringent, did not extend their daily activity time, contrary to expectations. It was in fact the small group that displayed extended daily activity during springtime, being active for 12 hours per day as opposed to 10.5 hours in the medium sized group and only 8.5 hours in the large group. Members of the large (n = 27) and medium-sized (n = 17) groups may experience greater pressure to remain inactive for longer due to higher levels of intraspecific food competition. Differences in the thermal properties of their respective crevices and in climatic conditions during the respective observation periods need to be investigated in more detail. Data does however suggest that the threshold where emergence becomes energetically viable is highly dependent on group size.

A unique feature of the daily activity patterns of *C. cataphractus* is the distinct late afternoon activity peaks around sunset, particularly evident during the dry season. In many cases it became too dark for the observer to see the lizards. The significance of this crepuscular behaviour is unclear at present and requires further investigation. One possibility is that this behaviour allows the lizards to utilize an additional class of invertebrate prey active only during this time of day. Alternatively, dusk is the time that lizards prefer to go on lengthy foraging sprees to escape group competition, relying on their unique tail-biting behaviour for defense. This antipredatory mechanism will only be effective when the lizards are some distance from the crevice. Close to the crevice, where they have been shown to spend most of their time, the lizards can quickly retreat into the crevice and tail-biting is superfluous. An analysis of group stability (Chapter 3) indicated that there is considerable movement of lizards among groups, but during 109 of the observation hours not a single

'moving' lizard was recorded. Such activity possibly takes place after sunset, eliminating birds of prey (with the exception of owls) as potential predators against which tail-biting behaviour is not very effective. Tail-biting would, however, be effective against terrestrial predators such as snakes and small mammals which display crepuscular activity.

In summary, *Cordylus cataphractus* restricts activity to the wet season when food availability is high. Even during periods of activity, lizards spend most of their time extremely close to the crevice. This is seen as a survival strategy within the constraints imposed upon the species by its group-living lifestyle. Individuals living in large groups experience greater pressure to meet energetic demands and take greater risks to forage successfully. Crepuscular activity is a possible adaptation allowing foraging and dispersive excursions, or possible exploitation of additional food resources. This behaviour warrants further investigation.

- GENERAL SUMMARY -

In the first chapter it was established that *Cordylus cataphractus* lizards are not forced to live in groups due to a limitation of refuge sites in their natural habitat. It is still a matter of speculation whether this group-living phenomenon is caused by a restriction of alternative resources, or whether individuals gain sufficient fitness benefits from conspecific proximity. In a temporally variable habitat such as experienced by this species, especially when food and water resources are limited, dispersal of individuals would be favoured. Group individuals are indeed more mobile than was previously suspected, with high rates of intergroup movement being recorded (Chapter 3). The fact that grouping behaviour nevertheless persists, suggests that mutual conspecific attraction might render individual benefits.

Mate accessibility is one proposed benefit to grouping behaviour, although this hypothesis is unconvincing in light of the high movement rate of lizards observed in this study. A similar argument applies to delayed dispersal of juveniles, since juveniles moved about no less between groups than adults. One plausible benefit to grouping behaviour is increased vigilance, which reduces the risk of predation, especially from raptors. Despite (possibly due to) their sluggish nature and heavy armour, armadillo lizards are extremely wary with a keen eyesight. As Peers (1930) puts it succinctly, entire groups often disappear "like magic" at the first sign of danger. Such vigilance would be greatly enhanced by the grouping effect and predation risk is further reduced by the dilution effect.

Keen eyesight is indeed of primary importance to *C. cataphractus*. Eyesight not only aids in predator detection, but plays a vital role in intraspecific communication and foraging ecology. Contrary to its solitary living congener, *C. cordylus*, *C. cataphractus* is unable to detect substrate pheromonal deposits from conspecifics (Chapter 2). This is not surprising, as substrate chemical signals may easily become clouded in the dense aggregations formed by this species. Visual cues are used as primary identification tools, supplemented by direct

tongue-flicking of conspecifics when required (own observations). Identification of individual group members may be important in assessment of, for instance, social status and sexual receptivity.

As mentioned, visual cues are also of prime importance to an extreme sit-and-wait forager. A sit-and-wait foraging strategy however poses severe problems to group-living lizards. Intraspecific competition for food items is intense, especially during times of prey scarcity and in larger groups. This is a major cost to group-living and *C. cataphractus* possesses several traits which are apparent adaptations to reduce energy expenditure. Physiologically, armadillo lizards possess a low resting metabolic rate and low fecundity as opposed to those of sympatric congenerics. Extraordinarily large fat bodies store energy for times of food scarcity. Behaviourally, as seen in this study, lizards remain fairly inactive throughout the year and only emerge from quiescence to forage and mate after the first winter rains bring about a flurry of insect life.

Such adaptations however seem costly to evolve and could as easily have emerged in response to an arid environment or food scarcity (as opposed to a group-living nature, per se). Predation pressure is required to be severe in order for the benefit of increased vigilance alone to offset the aforementioned costs. The cryptic colouration, heavy armour and tail-biting behaviour of *C. cataphractus*, further defensive adaptations, support this hypothesis. Severe predation pressure, combined with a historic incident of restriction in available refuges, provides one possible explanation for the evolution of a group-living nature in *C. cataphractus*.

Many questions remain unanswered. What factors cause individuals to leave their groups? When do these movements occur? Despite all the indirect evidence supporting intergroup movements, both inside and out of the mating season, such events have never been witnessed. Particularly enigmatic is the fact that these movements occur even during the

warm summer / autumn months, when the lizards are rarely observed outside of their crevice. What social structure exists within large groups of *C. cataphractus*? Is there selective partitioning of food resources, with males and females, adults and juveniles, or lizards of various social statuses feeding at different times of day? These are only a few of the questions that will hopefully be addressed in the near future and provide us with new insights on the life history of this charismatic South African lizard.

- LITERATURE CITED -

ABTS, M.L. 1987. Environment and variation in life history traits of the chuckwalla, *Sauromalus obesus*. *Ecological Monographs* **57**: 215-232.

ACOCKS, J.P.H. 1988. Veld types of South Africa. *Memoirs Botanical Survey of South Africa* **57**: 1-146.

ALBERTS, A.C. 1989. Ultraviolet visual sensitivity in desert iguanas: implications for pheromone detection. *Animal Behavior* **38**: 129-137.

ALBERTS, A.C. 1990. Chemical properties of femoral gland secretions in the Iguana, *Dipsosaurus dorsalis*. *Journal of Chemical Ecology* **16**: 13-25.

ALBERTS, A.C. 1991. Phylogenetic and adaptive variation in femoral gland secretions. *Copeia* **1991**: 69-79.

ALBERTS, A.C. 1992. Pheromonal self-recognition in desert iguanas. *Copeia* **1992**: 229-232.

ALBERTS, A.C. & WERNER, D.I. 1993. Chemical recognition of unfamiliar conspecifics by green iguanas: functional significance of different signal components. *Animal Behavior* **46**: 197-199.

ALEXANDER, R.S. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* **5**: 325-383.

ANDERSON, R.A. 1994. Functional and population responses of the lizard *Cnemidophorus tigris* to environmental fluctuations. *American Zoologist* **34**: 409-421.

ARNOLD, S.J. & WASSERSUG, R.J. 1978. Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): social behavior as a possible defense. *Ecology* **59**: 1014-1022.

AVERY, R.A. 1978. Activity patterns, thermoregulation and food consumption in two sympatric lizard species (*Podarcis muralis* and *P. sicula*) from central Italy. *Journal of Animal Ecology* **47**: 143-158.

BAUWENS, D., CASTILLA, A.M. &. MOUTON, P. LE F.N. 1999. Field body temperatures, activity levels and opportunities for thermoregulation in an extreme microhabitat specialist, the girdled lizard (*Cordylus macropholis). Journal of Zoology, London* **249**: 11-18.

BENSCH, S. & HASSELQUIST, D. 1991. Territory infidelity in the polygenous great reed warbler *Acrocephalus arundinaceus*: the effect of variation in territory attractiveness. *Journal of Animal Ecology* **60**: 857-871.

BISSINGER, B.E. & SIMON, C.A. 1979. Comparison of tongue-extrusions in representatives of six families of lizards. *Journal of Herpetology* **13**: 133-139.

BISSINGER, B.E. & SIMON, C.A. 1981. The chemical detection of conspecifics by juvenile Yarrow's spiny lizard, *Sceloporus jarrovi. Journal of Herpetology* **15**: 77-81.

BOCK, B.C. & RAND, A.S. 1989. Factors influencing nesting synchrony and hatching success at a green iguana nesting aggregation in Panama. *Copeia* **1989**: 978-986.

BONNETT, M. 1999. The ecology, behaviour and genetic relationships of a population of *Egernia striolata.* Unpublished PhD thesis. Flinders University of South Australia, Adelaide.

BRANCH, W.R. 1988a. *Field guide to the snakes and other reptiles of southern Africa.* Struik Publishers, Cape Town.

BRANCH, W.R. 1988b. South African Red Data Book – Reptiles and Amphibians. *South African National Scientific Programmes Report* No. 151. CSIR, Pretoria.

BRANCH, W.R. 1998. *Field Guide to Snakes and Other Reptiles of Southern Africa.* Struik Publishers, Cape Town.

BRANCH, W.R. & WHITING, M.J. 1997. A new *Platysaurus* (Squamata: Cordylidae) from the Northern Cape Province, South Africa. *African Journal of Herpetology* **46**: 124-136.

BROADLEY, D.G. 1978. A revision of the genus *Platysaurus* A. Smith (Sauria: Cordylidae). *Occasional Papers of the National Museum of Rhodesia, Series B* **6**: 131-185.

BULL, C.M. 1994. Population dynamics and pair fidelity in sleepy lizards. In: *Lizard Ecology: Historical and Experimental Perspectives*, (eds.) L.J. Vitt & E.R. Pianka, pp. 159-174. Princeton University Press, Princeton.

BULL, C.M., GRIFFIN, C.L., LANHAM, E.J. & JOHNSTON, G.R. 2000. Recognition of pheromones from group members in a gregarious lizard, *Egernia stokesii*. *Journal of Herpetology* **34**: 92-99.

BURGHARDT, G.M., GREENE, H.W. & RAND, A.S. 1977. Social behavior in hatchling green iguanas: life at a reptile rookery. *Science* **195**: 689-691.

BURGHARDT, G.M. & RAND, A.S. 1982. *Iguanas of the World: Their Behavior, Ecology, and Conservation*. Noyes Publications, New Jersey.

BURGHARDT, G.M. & RAND, A.S. 1985. Group size and growth rate in hatchling green iguanas (*Iguana iguana*). *Behavioral Ecology and Sociobiology* **18**: 101-104.

BURNS, T.A. 1970. Temperature of Yarrow's spiny lizard *Sceloporus jarrovi* at high altitudes. *Herpetologica* **26**: 9-16.

BURRAGE, B.R. 1974. Population structure in *Agama atra* and *Cordylus cordylus* in the vicinity of De Kelders, Cape Province. *Annals of the South African Museum* **66**: 1-23.

CAMP, C.L. 1923. Classification of the lizards. *Bulletin of the American Museum of Natural History* **48**: 289-481.

CARPENTER, G.C. 1975. The ecology and social behavior of the chuckwalla, *Sauromalus obesus obesus* Baird. *Copeia* **1975**: 388-389.

CARPENTER, G.C. & DUVALL, D. 1995. Fecal scent marking in the western banded gecko (*Coleonyx variegatus*). *Herpetologica* **51**: 33-38.

CARPENTER, G.C. & FERGUSSON, G.W. 1977. Variation and evolution of stereotyped behavior in reptiles. In: *Biology of the Reptilia*, (ed.) C. Gans & D.W. Tinkle, Vol. 7, pp. 335-554. Academic Press, London.

COLE, C.J. 1966. Femoral glands in lizards: a review. *Herpetologica* **22**: 199-206.

CONNELL, S.D. 2000. Is there safety in numbers for prey? *Oikos* **88**: 527-532.

COOPER, W.E., Jr. 1989. Absence of prey odor discrimination by iguanid and agamid lizards in applicator tests. *Copeia* **1989**: 472-478.

COOPER, W.E., Jr. 1994. Prey chemical discrimination, foraging mode, and phylogeny. In: *Lizard Ecology: Historical and Experimental Perspectives*, (eds.) L.J. Vitt & E.R. Pianka, pp. 95-116. Princeton University Press, Princeton.

COOPER, W.E., Jr., GARSTKA, W.R. & VITT, L.J. 1986. Female sex pheromone in the lizard *Eumeces laticeps*. *Herpetologica* **42**: 361-366.

COOPER, W.E., Jr. & TRAUTH, A.E. 1992. Discrimination of conspecific male and female cloacal chemical stimuli by males and possession of a probable pheromone gland by females in a cordylid lizard, *Gerrhosaurus nigrolineatus*. *Herpetologica* **48**: 229-236.

COOPER, W.E., Jr., VAN WYK, J.H. & MOUTON, P. LE F.N. 1996. Pheromonal detection and sex-discrimination of conspecific substrate deposits by the rock-dwelling lizard *Cordylus cordylus*. *Copeia* **1996**: 839-845.

COOPER, W.E., Jr. & VITT, L.J. 1984. Detection of conspecific odors by the female broad-headed skink, *Eumeces laticeps*. *Journal of Experimental Zoology* **229**: 49-54.

COOPER, W.E., Jr., WHITING, M.J. & VAN WYK, J.H. 1997. Foraging modes of cordyliform lizards. *South African Journal of Zoology* **32**: 9-13.

CORDES, I.G., MOUTON, P. LE F.N. & VAN WYK, J.H. 1995. Sexual dimorphism in two girdled lizard species, *Cordylus niger* and *C. cordylus*. *South African Journal of Zoology* **30**: 187-196.

COWLES, R.B. & PHELAN, R.L. 1958. Olfaction in rattlesnakes. *Copeia* **1958**: 73-83.

DAVIS, J.A. & BROWN, C.R. 2000. Costs of coloniality and the effect of colony size on reproductive success in Purple Martins. *Condor* **101**: 737-745.

DEFAZIO, A., SIMON, C.A., MIDDENDORF, G.A. & ROMANO, D. 1977. Iguanid substrate licking: a response to novel situations in *Sceloporus jarrovi*. *Copeia* **1977**: 706-709.

DOBSON, F.S. 1982. Competition for mates and predominant male juvenile dispersal in mammals. *Animal Behavior* **30**: 1183-1192.

DUFFIELD, G.A. & BULL, C.M. 2001. Stable social aggregations in an Australian lizard, *Egernia stokesii*. Submitted to Behavioral Ecology and Sociobiology.

DUVALL, D., HERSKOWITZ, R. & TRUPIANO-DUVALL, J. 1980. Responses of five-lined skinks (*Eumeces fasciatus*) and ground skinks (*Scincella lateralis*) to conspecific and interspecific chemical cues. *Journal of Herpetology* **14**: 121-127.

DUVALL, D., TRUPIANO, J. & SMITH, H.M. 1979. An observation of maternal behavior in the Mexican desert spiny lizard, *Sceloporus rufidorsum*. *Transactions of the Kansas Academy of Science* **82**: 60-62.

ESTES, R., GAUTHIER, J. & DE QUEIROZ, K. 1988. Phylogenetic relationships within Squamata. In: *Phylogenetic Relationships of the Lizard Families, Essays Commemorating Charles L. Camp*, (eds.) R. Estes & G. Pregill, pp. 119-282. Stanford University Press, Stanford.

EVANS, L.T. 1959. A motion picture study of maternal behavior of the lizard *Eumeces obsoletus* Baird and Baird. *Copeia* **1959**: 103-110.

FERGUSSON, B., BRADSHAW, S.D. & CANNON, J.R. 1985. Hormonal control of femoral gland secretion in the lizard, *Amphibolurus ornatus. General and Comparative Endocrinology* **57**: 371-376.

FITZSIMONS, V.F. 1943. The lizards of South Africa. *Transvaal Museum Memoirs* **1**: 1-528.

FLEMMING, A.F. & VAN WYK, J.H. 1992. The female reproductive cycle of the lizard *Cordylus p. polyzonus* (Sauria: Cordylidae) in the Southwestern Cape Province, South Africa. *Journal of Herpetology* **26**: 121-127.

FOÀ, A., TOSINI, G. & AVERY, R. 1992. Seasonal and diel cycles of activity in the ruin lizard, *Podarcis sicula. Herpetological Journal* **2**: 86-89.

FROST, D., JANIES, D., MOUTON, P. LE F.N. & TITUS, T. 2001. A molecular perspective on the phylogeny of the girdled lizards (Cordylidae, Squamata). *American Museum Novitates* **3310**: 1-10.

GRANT, B.W. & DUNHAM, A.E. 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami. Ecology* **69**: 167-176.

GRAVELLE, K. & SIMON, C.A. 1980. Field observations on the use of the tongue-Jacobson's organ system in two iguanids, *Sceloporus jarrovi* and *Anolis trinitatis. Copeia* **1980**: 356-359.

GRAVES, B.M. & DUVALL, D. 1993. Reproduction, rookery use, and thermoregulation in free-ranging, pregnant *Crotalus v. viridis. Journal of Herpetology* **27**: 33-41.

GRAVES, B.M. & DUVALL, D. 1995. Aggregation of squamate reptiles associated with gestation, oviposition, and parturition. *Herpetological Monographs* **9**: 102-119.

GRAVES, B.M. & HALPERN, M. 1989. Chemical access to the vomeronasal system of the lizard *Chalcides ocellatus*. *Journal of Experimental Zoology* **249**: 150-157.

GRAVES, B.M. & HALPERN, M. 1991. Discrimination of self from conspecific chemical cues in *Tiliqua scincoides* (Sauria: Scincidae). *Journal of Herpetology* **25**: 125-126.

GREENBERG, B. 1943. Social behavior of the western banded gecko, *Coleonyx variegatus* Baird. *Physiological Zoology* **16**: 110-122.

GREENWOOD, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behavior* **28**: 1140-1162.

GREENWOOD, P.J. & HARVEY, P.H. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* **13**: 1-21.

GREGORY, P.T., MACARTNEY, J.M. & LARSEN, K.W. 1987. Spatial patterns and movements. In: *Snakes: Ecology and Evolutionary Biology*, (eds.) R.A. Seigel, J.T. Collins & S.S. Novak, pp. 366-395. McGraw-Hill, New York.

HAMILTON, W.J. 1948. Hibernation site of the lizards *Eumeces* and *Anolis* in Louisiana. *Copeia* **1948**: 211.

HARVEY, M.B. & GUTBERLET, R.L., Jr. 1995. Microstructure, evolution, and ontogeny of scale surfaces in cordylids and gerrhosaurid lizards. *Journal of Morphology* **226**: 121-139.

HEATWOLE, H., LIN, T.H., VILLALÓN, E., MUÑIZ, A. & MATTA, A. 1969. Some aspects of the thermal ecology of Puerto Rican anoline lizards. *Journal of Herpetology* **3**: 65-77.

HENSON, W.R. 1959. Some effects of secondary dispersive processes on distribution. *American Naturalist* **93**: 315-320.

HOOFIEN, J.H. 1962. An unusual congregation of the gekkonid lizard *Tarentola annularis* (Geoffroy). *Herpetologica* **18**: 54-56.

HOUSE, S.M., TAYLOR, P.J. & SPELLERBERG, I.F. 1980. Patterns of daily behavior in two lizard species *Lacerta agilis* L. and *Lacerta vivipara* Jacquin. *Oecologia* **44**: 396-402.

HUEY, R.B. 1982. Temperature, physiology, and the ecology of reptiles. In: *Biology of the Reptilia* (eds.) C. Gans & D. Crews, Vol. 12, pp. 25-91. Academic Press, New York.

HUTCHINSON, M.N. 1993. Family Scincidae. In: *Fauna of Australia - Amphibia and Reptilia* (eds.) C.J. Glasby, G.J.B. Ross & B.L. Beesley, Vol. 2A, pp. 261-279. Australian Government Publishing Service, Canberra.

JACOBSEN, N.H.G., NEWBERY, R.E. & PETERSEN, W. 1990. On the ecology and conservation status of *Cordylus giganteus* A. Smith in the Transvaal. *South African Journal of Zoology* **25**: 61-66.

JOHNSON, M.L. & GAINES, M.S. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics* **21**: 449-480.

KARLSON, P. & LUSCHER, M. 1959. Pheromones: a new term for a class of biologically active substances. *Nature* **183**: 55-56.

KYLE, R. & ROBERTSON, W.D. 1997. Preliminary estimates of population size and capture rates of mature *Acanthopagrus berda* in the Kosi lakes system, South Africa, using mark-recapture methods. *South African Journal of Zoology* **32**: 124-128.

LABURN, H.P., MITCHELL, D., KENEDI, E. & LOUW, G.N. 1981. Pyrogens fail to produce fever in a cordylid lizard. *American Journal of Physiology* **241**: R198-R202.

LANG, M. 1991. Generic relationships within Cordyliformes (Reptilia, Squamata). *Bulletin de l'Institut Royal des Sciences Naturelles Belges, série Biologie* **61**:121-188.

LEMOS-ESPINAL, J.A., BALLINGER, R.E., SARABIA, S.S. & SMITH, G.R. 1997. Aggregation behavior of the lizard *Sceloporus mucronatus mucronatus* in Sierra del Ajusco, México. *Herpetological Review* **28**: 126-127.

LIDICKER, W.Z., Jr. 1975. The role of dispersal in the demography of small mammals. In: *Small Mammals: Productivity and Dynamics of Populations*, (eds.) K. Petrusewicz, E.B. Golley & L. Ryszkowski, pp. 103-128. Cambridge University Press, London.

LOVERIDGE, A. 1944. Revision of the African lizards of the family Cordylidae. *Bulletin of the Museum of Comparative Zoology at Harvard University* **95**: 1-118.

MAIN, A.R. & BULL, M. 1996. Mother-offspring recognition in two Australian lizards, *Tiliqua rugosa* and *Egernia stokesii*. *Animal Behavior* **52**: 193-200.

MALAN, M.E. 1946. Contributions to the comparative anatomy of the nasal capsule and the organ of Jacobson of the Lacertilia. *Annals of the University of Stellenbosch* **24**: 69-137.

MASON, R.T. 1992. Reptilian pheromones. In: *Biology of the Reptilia*, (eds.) C. Gans & D. Crews, Vol. 18, pp. 114-228. University of Chicago Press, Chicago.

MCCULLOUGH, C. 1998. *Caesar*. Century, London.

MCRAE, S. 1996. Family values: costs and benefits of communal nesting in the moorhen. *Animal Behavior* **52**: 225-245.

MILSTEAD, W.W. 1970. Late summer behavior of the lizards *Sceloporus merriami* and *Urosaurus ornatus* in the field. *Herpetologica* **26**: 343-354.

MOUTON, P. LE F.N. 1987. Phenotypic variation among populations of *Cordylus cordylus* (Reptilia: Cordylidae) in the south-western Cape Province, South Africa. *South African Journal of Zoology* **22**: 119-129.

MOUTON, P. LE F.N. 1988. *Cordylus cataphractus*: species account. In*: South African Red Data Book – Reptiles and Amphibians*, (ed.) W.R. Branch, South African National Scientific Programmes Report, 151 p.

MOUTON, P. LE F.N., FLEMMING, A.F. & KANGA, E.M. 1999. Grouping behaviour, tail-biting behaviour, and sexual dimorphism in the armadillo lizard (*Cordylus cataphractus*) from South Africa. *Journal of Zoology, London* **249**: 1-10.

MOUTON, P. LE F.N., FLEMMING, A.F. & NIEWOUDT, C.J. 2000a. Sexual dimorphism and sex ratio in a terrestrial girdled lizard, *Cordylus macropholis. Journal of Herpetology* **34**: 379-386.

MOUTON, P. LE F.N., FOURIE, D. & FLEMMING, A.F. 2000b. Oxygen consumption in two cordylid lizards, *Cordylus cataphractus* and *Cordylus polyzonus. Amphibia-Reptilia* **21**: 502-507.

MOUTON, P. LE F.N., GEERTSEMA, H. & VISAGIE, L. 2000c. Foraging mode of a group-living lizard, *Cordylus cataphractus* (Cordylidae). *African Zoology* **35**: 1-7.

MOUTON, P. LE F.N. & OELOFSEN, B.W. 1988. A model explaining patterns of geographic character variation in *Cordylus cordylus* (Reptilia: Cordylidae) in the south-western Cape, South Africa. *South African Journal of Zoology* **23**: 20-31.

MOUTON, P. LE F.N., OELOFSEN, B.W. & MOSTERT, D.P. 1987. New data on threatened lizard species in the south-western Cape. *South African Journal of Science* **83**: 48-52.

MOUTON, P. LE F.N. & VAN WYK, J.H. 1993. Sexual dimorphism in cordylid lizards: a case study of the Drakensberg crag lizard, *Pseudocordylus melanotus. Canadian Journal of Zoology* **71**: 1715-1723.

MOUTON, P. LE F.N. & VAN WYK, J.H. 1997. Adaptive radiation in cordyliform lizards: An overview. *African Journal of Herpetology* **46**: 78-88.

MYRES, B.C. & EELLS, M.M. 1968. Thermal aggregation in *Boa constrictor*. *Herpetologica* **24**: 61-66.

NEILL, W.T. 1948. Hibernation of amphibians and reptiles in Richmond County, Georgia. *Herpetologica* **4**: 107-114.

NELSON, K.J. & GREGORY, P.T. 2000. Activity patterns of garter snakes, *Thamnophis sirtalis*, in relation to weather conditions at a fish hatchery on Vancouver Island, British Columbia. *Journal of Herpetology* **34**: 32-40.

NEWTON, I. 1993. Age and site fidelity in female sparrowhawks *Accipiter nisus. Journal of Animal Ecology* **46**: 161-168.

NEWTON, I. & MARQUISS, M. 1982. Fidelity to breeding area and mate in sparrowhawks *Accipiter nisus*. *Journal of Animal Ecology* **51**: 327-341.

PÄRT, T. & GUSTAFSSON, L. 1989. Breeding dispersal in the collared flycatcher (*Ficedula albicollis*): possible causes and reproductive consequences. *Journal of Animal Ecology* **58**: 305-320.

PEERS, B. 1930. A record of the peculiarities of the lizard *Zonurus cataphractus* (Boie), as observed during travels in Namaqualand in May 1928. *South African Journal of Natural History* **VI**: 402-411.

PETERSON, C.R., GIBSON, A.R. & DORCAS, M.E. 1993. Snake thermal ecology: the causes and consequences of body temperature variation. In: *Snakes: Ecology and Behavior*, (eds.) R.A. Siegel and J.T. Collins, pp. 241-314. McGraw-Hill, New York.

POPE, C.H. 1937. *Snakes alive and how they live*. Viking Press, New York.

PORTER, W.P. & TRACY, C.R. 1983. Biophysical analyses of energetics, time-space utilization and distributional limits. In: *Lizard Ecology: Studies of a Model Organism*, (eds.) R.B. Huey, E.R. Pianka & T.W. Schoener, pp. 55-83. Harvard University Press, Cambridge.

POWELL, H., HEATWOLE, H. & HEATWOLE, M. 1977. Winter aggregation of *Leiolopisma guichenotti*. *British Journal of Herpetology* **5**: 789-791.

PRATT, C.W. 1948. The morphology of the ethmoidal region of *Sphenodon* and lizards. *Proceedings of the Zoological Society of London* **118**: 171-201.

PULLIAM, H.R., DUNNING, J.B. & LIU, J. 1992. Population dynamics in complex landscapes: a case study. *Ecological Applications* **2**: 165-177.

RAND, A.S. 1967. Communal egg-laying in anoline lizards. *Herpetologica* **23**: 227-230.

ROSE, B. 1981. Factors affecting activity in *Sceloporus virgatus*. *Ecology* **62**: 706-716.

RUBY, D.E. 1977. Winter activity in Yarrow's spiny lizard, *Sceloporus jarrovi*. *Herpetologica* **33**: 322-333.

RUDDOCK, L., VAN WYK, J.H. & CHERRY, M.I. 2001. Territoriality in the lizard *Cordylus cordylus* (Sauria: Cordylidae). *Journal of Herpetology* (in press).

SCHOENER, T.W. 1970. Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* **51**: 408-418.

SCHOENER, T.W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* **2**: 369-404.

SCHOENER, T.W. 1977. Competition and the niche. In: *Biology of the Reptilia*, (ed.) C. Gans & D.W. Tinkle, Vol. 7, pp. 335-554. Academic Press, London.

SEARCY, W.A. 1979. Female choice of mates: a general model for birds and its application to red-winged blackbirds (*Agelaius phoeniceus*). *American Naturalist* **114**: 77-100.

SEBURN, C.N.L. 1993. Spatial distribution and microhabitat use in the five-lined skink (*Eumeces fasciatus*). *Canadian Journal of Zoology* **71**: 445-450.

SIMON, C.A. 1983. A review of lizard chemoreception. In: *Lizard Ecology: Studies of a Model Organism*, (eds.) R.B. Huey, E.R. Pianka & T.W. Schoener, pp. 119-133. Harvard University Press, Cambridge.

SIMON, C.A. 1985. Chemoreception in *Sceloporus jarrovi*: does olfaction activate the vomeronasal system? *Copeia* **1985**: 239-242.

SIMON, C.A., GRAVELLE, K., BISSINGER, B.E., EISS, I. & RUIBAL, R. 1981. The role of chemoreception in the iguanid lizard *Sceloporus jarrovi*. *Animal Behavior* **29**:46-54.

SIMON, C.A. & MIDDENDORF, G.A. 1976. Resource partitioning by an iguanid lizard: temporal and microhabitat aspects. *Ecology* **57**: 1317-1320.

SMITH, G.R. 1996. Annual life-history variation in the striped plateau lizard, *Scelloporus virgatus*. *Canadian Journal of Zoology* **74**: 2025-2030.

SMITH, G.R., BALLINGER, R.E. & ROSE, B. 1995. Reproduction in *Sceloporus virgatus* from the Chiricahua Mountains of south-eastern Arizona, with emphasis on annual variation. *Herpetologica* **51**: 342-349.

SOUTHWOOD, T.R.E. 1978. *Ecological Methods – With Particular Reference to the Study of Insect Populations*. Chapman & Hall, London.

SWITZER, P.V. 1993. Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology* **7**: 533-555.

SWITZER, P.V. 1997a. Factors affecting site fidelity in a territorial animal, *Perithemis tenera*. *Animal Behavior* **53**: 865-877.

SWITZER, P.V. 1997b. Past reproductive success affects future habitat selection. *Behavioral Ecology and Sociobiology* **40**: 307-312.

TAYLOR, L.R. & TAYLOR, R.A.J. 1977. Aggregation, migration and population mechanics. *Nature* **265**:415-421.

TINKLE, D.W. & HADLEY, N.F. 1973. Reproductive effort and winter activity in the viviparous montane lizard *Sceloporus jarrovi*. *Copeia* **1973**: 272-277.

TOFT, C.A. 1985. Resource partitioning in amphibians and reptiles. *Copeia* **1985**: 1-21.

VAN WYK, J.H. 1989. The female reproductive system of the lizard, *Cordylus polyzonus polyzonus* (Sauria: Cordylidae) in the Orange Free State. *South African Journal of Zoology* **24**: 263-269.

VAN WYK, J.H. 1990. Seasonal testicular activity and morphometric variation in the femoral glands of the lizard *Cordylus polyzonus polyzonus* (Sauridae: Cordylidae). *Journal of Herpetology* **24**: 405-409.

VAN WYK, J.H. 1992. Life history and physiological ecology of the lizard, *Cordylus giganteus*. Ph.D. dissertation, University of Cape Town, Cape Town, South Africa.

VAN WYK, J.H. & MOUTON, P. LE F.N. 1992. Glandular epidermal structures of cordylid lizards. *Amphibia-Reptilia* **13**: 1-12.

VAN WYK, J.H. & MOUTON, P. LE F.N. 1998. Reproduction and sexual dimorphism in the montane viviparous lizard, *Pseudocordylus capensis* (Sauria: Cordylidae). *South African Journal of Zoology* **33**: 156-165.

VILLARD, M.–A., MERRIAM, G. & MAURER, B.A. 1995. Dynamics in subdivided populations of neotropical migratory birds in a fragmented temperate forest. *Ecology* **76**: 27-40.

VITT, L.J. 1974. Winter aggregations, size classes, and relative tail breaks in the tree lizard, *Urosaurus ornatus ornatus* (Sauria: Iguanidae). *Herpetologica* **30**: 182-183.

WEATHERHEAD, P.J. & HOYSAK, D.J. 1989. Spatial and activity patterns of black rat snakes (*Elaphe obsolete*) from radiotelemetry and recapture data. *Canadian Journal of Zoology* **67**: 463-468.

WEINTRAUB, J.D. 1968. Winter behaviour of the granite spiny lizard, *Sceloporus orcutti* Stejneger. *Copeia* **1968**: 708-712.

WERNER, D., BAKER., E., GONZALEZ, E. DEL C. & SOSA, I.R. 1987. Kinship recognition and grouping in hatchling green iguanas. *Behavioral Ecology and Sociobiology* **21**: 83-89.

WIRMINGHAUS, J.O. 1990. Observations on the behaviour of the Cape girdled lizard *Cordylus cordylus* (Reptilia: Cordylidae). *Journal of Natural History* **24**: 1617-1627.

WORTHINGTON, R.D. & SABATH, M.D. 1966. Winter aggregations of the lizard *Urosaurus ornatus ornatus* (Baird and Girard) in Texas. *Herpetologica* **22**: 94-96.

- APPENDIX A -

The following data set was recorded for a group of *Cordylus cataphractus* consisting of 40 individuals. This constitutes the largest group of this species that has been collected to date. Thirty-nine individuals were toe-clipped and released at their site of capture. One lizard escaped, and data on this individual is not included below.

SPECIES: *Cordylus cataphractus*

LOCALITY: 3118CC&CD Doringbaai (31° 55' 17" S; 18° 21' 34" E)

COLLECTION DATE: 27 November 1998

COLLECTORS: L. Visagie, A. Strydom, L. Ruddock, A. Searby,

MICROHABITAT: Single, loose-standing sandstone rock (1 x 0.8 x 0.4 m) resting obliquely on a larger rock base.

METHOD: Lifted single large rock with crowbar; lizards were captured by hand, or noosed.

KEY TO TABLES:

LF = Left front foot; RF = Right front foot

LB = Left back foot; RB = Right back foot.

M = Male; F = Female; U = Unsure

SVL = snout-vent length (mm)

HW = head width (mm); HL = head length (mm); HD = head depth (mm)

LFg = left leg femoral gland total; RFg = right leg femoral gland total

LGg = left leg generation gland total; RGg = right leg generation gland total

Lizard ID	Toe clip	Lizard ID	Toe clip
1	LF2,RF2	21	LF2,RB4
2	LF2,RF3	22	LF3,RB2
3	LF2,RF4	23	LF3,RB3
4	LF3,RF2	24	LF3,RB4,RB3,RB5
5	LF3,RF3,LF2	25	LF4,RB2
6	LF3,RF4	26	LF4,RB3
7	LF4,RF2	27	LF4,RB4
8	LF4,RF3	28	RF2,RB2
9	LF2,LB2	29	RF2,RB3
10	LF4,RF4	30	RF2,RB4
11	LF2,LB3	31	RF3,RB2
12	LF2,LB4	32	RF3,RB2
13	LF3,LB2	33	RF3,RF2,RB4
14	LF3,LB3	34	RF4,RB2
15	LF3,LB4	35	RF4,RB3
16	LF4,LB2	36	RF4,RB4
17	LF4,LB3	37	LF5,RB1
18	LF4,LB4	38	LF5,RB2
19	LF2,RB2	39	LF5,RB3
20	LF2,RB2,RB3		

Lizard ID	Sex	SVL (mm)	LFg	RFg	LGg	RGg	Scars
1		67	9	8	0	0	Tail regenerated
2		70	8	9	6	7	
3	F	107	U	U	U	U	
4	M	110	U	U	U	U	
5	M	115	U	U	U	U	
6		72	11	12	29	28	
7		63	13	13	0	0	
8		76	11	12	31	28	
9		72	16	15	0	0	
10		72	14	15	0	0	
11		78	15	15	21	20	
12		67	14	16	0	0	
13		90	15	16	11	8	Tail regenerated
14		54	14	11	16	19	
15		85	13	13	0	0	
16		83	15	15	7	9	
17		91	16	15	53	48	Tail regenerated
18	M	96	13	14	25	30	
19		93	13	13	0	0	
20	F	97	14	13	5	8	
21	U	95	13	13	16	14	
22	F	104	16	15	4	2	
23	F	100	11	12	1	4	
24		93	13	11	2	0	Tail regenerated
25	F	109	16	13	5	10	Tail regenerated
26	F	105	14	12	3	5	
27	U	99	15	15	8	8	
28		91	14	14	0	0	
29	U	95	14	13	4	6	
30		92	14	15	0	2	Tail regenerated
31	F	98	15	13	6	9	
32	F	102	15	14	4	6	
33	M	113	16	17	20	25	
34	F	112	13	14	5	6	
35	F	100	13	13	2	5	
36	F	99	12	14	3	1	
37	F	109	15	14	8	7	
38	M	107	17	15	15	18	
39	F	109	14	13	2	1	

Lizard ID	Sex	SVL (mm)	Mass (g)	HW (mm)	HL (mm)	HD (mm)
1		67	12.47	17.11	18.50	8.00
2		70	12.12	16.63	19.38	8.94
3	F	107	52.62	27.62	27.96	11.55
4	M	110	65.90	30.19	31.36	16.59
5	M	115	76.68	33.92	31.80	15.38
6		72	14.64	17.69	18.72	8.60
7		63	10.22	14.21	16.68	7.53
8		76	14.03	17.58	19.67	7.01
9		72	14.09	18.53	20.95	8.62
10		72	10.71	17.18	20.44	8.40
11		78	21.57	20.66	21.31	10.28
12		67	12.21	15.40	18.86	8.85
13		90	29.46	23.44	25.57	11.68
14		54	23.59	28.18	23.87	11.37
15		85	27.83	21.99	23.99	11.58
16		83	24.12	21.51	22.79	10.56
17		91	31.66	23.98	25.03	12.71
18	M	96	31.91	25.18	27.80	12.45
19		93	37.75	34.09	26.03	10.90
20	F	97	35.73	24.83	26.04	11.60
21	U	95	35.85	25.28	26.02	11.13
22	F	104	50.16	27.41	28.22	13.09
23	F	100	44.57	26.89	26.34	13.11
24		93	28.77	23.33	24.99	11.99
25	F	109	59.37	28.51	26.32	13.69
26	F	105	48.81	27.70	28.35	14.54
27	U	99	39.72	25.01	28.67	11.37
28		91	30.74	26.43	25.72	11.33
29	U	95	34.71	23.38	23.36	14.13
30		92	31.67	25.43	25.06	12.11
31	F	98	46.89	28.39	28.58	13.86
32	F	102	49.75	28.29	27.25	13.55
33	M	113	70.07	34.32	32.23	14.75
34	F	112	49.09	28.77	28.32	13.12
35	F	100	54.97	30.17	29.88	12.87
36	F	99	55.59	29.53	28.51	13.87
37	F	109	56.75	29.53	29.48	11.96
38	M	107	59.28	30.69	29.78	13.82
39	F	109	56.26	28.35	28.08	12.28